AN ABSTRACT OF THE DISSERTATION OF

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Title: Explorations Into Who is Doing Freshwater Science and How We are Altering Waterscapes

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The United States of America and the world are faced with three massive intertwining challenges at this time: COVID-19, racial inequity, and climate change. As a species, humans must come together and collectively address these challenges to preserve our humanity and make our world a more just and livable place for all species. This dissertation presents research to support paths forward on addressing racial inequity in scientific societies and human alterations to freshwater ecosystems, two small components of the larger challenges we face. We must not get overwhelmed by the magnitude of the issues that face us; instead, we must deconstruct them into actionable parts that we as individuals and communities can address, issue by issue. While academic researchers are encouraged by institutions (whether explicitly or implicitly) to be narrowly focused on their scientific research, many researchers are challenging this constraining stance and are demanding the

freedom to study the contextual web surrounding their research. Scientists are stepping back and examining who is and who is not entering and remaining in their fields. Scientists are more and more often taking the time to place their work in the context of the world within which we live and consider the impacts of racial inequities and climate change both on their science, their fellow collaborators, and the public. My doctoral research and this dissertation reflect my efforts to model this approach to academic research as a graduate employee and scholar deeply concerned about our humanity.

First, I address racial inequity in scientific societies and provide a path for one scientific society of which I am a member to become more inclusive and diverse. Specifically, I, along with 10 co-authors, evaluated the demography within the Society for Freshwater Science (SFS; Chapter 2). Respondents overwhelmingly identified as white (87%). Women, respondents with disabilities, and individuals from marginalized racial backgrounds were underrepresented in SFS relative to the US population. Only 0.7% of SFS survey respondents identified as Black, although African Americans represented 6% of the US professoriate in 2015. People who identified as transgender and people who identified as LGBTQ+ constituted a higher percentage of survey respondents than those identifying as such among US adults. We acknowledge that concerted efforts are needed to recognize and challenge systemic discrimination to ensure scientists from marginalized groups can contribute to and benefit from scientific societies. To aid in these efforts, we presented a guide for SFS toward creating a more welcoming and equitable space for all scientists to do their research.

In addition to examining who is doing freshwater science, I, along with eight co-authors, examined how humans are altering freshwater ecosystems. Specifically, I quantified how dams in the Colorado River Basin are impacting aquatic invertebrate communities at the community (Chapter 3) and molecular (Chapter 4) levels. I found that each tailwater (i.e., the section of river downstream of a dam) was dominated by 3-7 invertebrate taxa that comprised 95% of individuals. Many of these dominant taxa were non-insect, non-flying species and thus were unavailable to terrestrial consumers. Consistent with previous studies, aquatic insects and sensitive EPT taxa (Ephemeroptera, Plecoptera, and Trichoptera) were negatively associated with hydropeaking intensity (magnitude of daily flow fluctuations associated with hydropower generation), which puts limits on the type and perhaps quality of the invertebrate food base. While total invertebrate abundance and biomass did not change with increasing distance from dam, insect and EPT richness, abundance, and biomass all increased, suggesting that impacts of damming are most acute immediately downstream of dams. Our results demonstrate that western U.S. tailwaters can support aquatic invertebrate communities with high abundance, yet low species diversity.

At the molecular level, I used 2bRAD genetics methods to determine genetic diversity, population structure, and evidence of fragmentation for three species of aquatic insects in the Grand Canyon that differed according to dispersal ability. Genetic results revealed that actual dispersal patterns may not always be accurately predicted by trait databases and distribution patterns for some widespread species. We found evidence that both *R. distincta* and *H. osleri* are relatively high dispersers, whereas *F. quilleri* is a moderate disperser. This finding is congruent with dispersal abilities predicted by trait database for *H. osleri* and *F. quilleri*, but contradicts information for *R. distincta*. Additionally, genetic diversity and relationships between genetic and geographic distance suggest the evolutionary mechanisms at play in a fragmented landscape for these species. *F. quilleri* exhibited isolation by distance, whereas *H. osleri* and *R. distincta* showed evidence of gene flow. Furthermore, *H. osleri* showed population structure between tributaries on the North Rim vs. South Rim. As genetic tools become cheaper and more powerful, researchers will be able to understand the movements of and more successfully conserve understudied organisms, such as aquatic insects, that are critical for the integrity of our ecosystems.

Ultimately my main dissertation chapters will be published as three scientific journal articles and contribute to the base of literature that organizers, activists, and conversation practitioners use to conserve our natural resources and make our scientific societies more just and equitable. Simply put, I have just provided the data. It is up to me and my readers to use these data to make substantial changes in how our human communities operate and how we as humans impact our environment. As a PhD student, I have begun this work, choosing to work with the Society for Freshwater Science to improve its meetings, working with the labor union of Oregon State graduate employees to create more equitable conditions for workers, and collaborating with the US Geological Survey which works closely with power companies operating dams. As a post-doc and later as a professional, I am committed to continuing this work in whatever context that I can. I believe that it is imperative that academic scientists take up the challenge of both analyzing the societal context surrounding their scientific research and making their labs, departments, universities, and communities more diverse and inclusive spaces. This is work that all humans must do, but academics are uniquely poised to do this work as people who are paid to think and do research. We must do some of the heavy lifting, as there are many, many folx who do not have the academic freedom that we are privileged enough to have. We must use that privilege to create a more just, equitable, sustainable, and loving society. Why else are we here?

Explorations Into Who is Doing Freshwater Science and How We are Altering Waterscapes

by

Erin Foster Abernethy

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I understand that my dissertation will become part of the permanent collection of Oregon State University libraries. My signature below authorizes release of my dissertation to any reader upon request.

Erin Foster Abernethy, Author

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CONTRIBUTION OF AUTHORS

Chapter 2 (Diverse, equitable, and inclusive scientific societies: Progress and opportunities in the Society for Freshwater Science): All authors conceived the study. AGB, MRC, MWS, and IA analyzed the SFS survey data. EFA, IA, AGB, CCG, MRC, EIL, EKM, AJS, and AJW drafted individual sections of the manuscript. CCG collected and analyzed Instars survey data. CCG, AJW, and EKM made the figures. EFA, AGB, EIL, and MRC combined individual sections into a cohesive manuscript. All authors edited the manuscript. EFA and AJS addressed reviewer comments.

Chapter 3 (Hydropeaking intensity and dam proximity limit aquatic invertebrate diversity in the Colorado River Basin): All authors conceived the study. JDM and TAK collected specimens. RVD identified invertebrates. EFA analyzed data and wrote the manuscript. JDM, TAK, JDT, and DAL edited the manuscript. EFA addressed reviewer comments.

Chapter 4 (Fragmentation and dispersal of aquatic insects in a regulated, desert river): EFA, JDM, TAK, MB, and DAL conceived the study. EFA collected specimens. EFA, KD, and HE completed molecular lab work and analysis. EFA wrote the manuscript. All authors edited the manuscript. EFA addressed reviewer comments.

Given the contributions of my co-authors, I use plural pronouns throughout Chapters 2, 3, and 4. Elsewhere, I use singular pronouns, as I am speaking solely for myself.

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Chapter 1 – General Introduction

For centuries, science has been a nearly-exclusive domain of upper-class white men, with limited opportunities for marginalized people to either make or be recognized for notable scientific contributions (Bronstein and Bolnick 2018). Marginalized people are discriminated against or oppressed based on characteristics such as race and ethnicity, class, religion, national origin, language, citizenship, marital status, sex, age, differing abilities, sexual orientation, gender identity and expression, transgender status, and parental or pregnancy status. Many scientific institutions still fail to adequately address the ways that societal systems of privilege and power operate to marginalize members of our communities (Brown et al. 2017, Potvin et al. 2018). As a result, most American scientific societies remain disproportionately white, male, heterosexual, and cisgender (George et al. 2001, Stevens et al. 2008, Beck et al. 2014, Arismendi and Penaluna 2016, Penaluna et al. 2017). This is now being recognized as a serious moral problem that should be remedied.

In Chapter 2, I discuss how the Society for Freshwater Science (SFS) and its members have worked to reduce barriers against diversity, equity, and inclusivity, and I highlight areas where additional progress will further advance this goal. In particular, I do the following: 1) review the function of diversity, equity, and inclusivity in scientific societies; 2) outline the current demographics and cultural climate within SFS; 3) describe 2 examples intended to increase diversity, equity, and inclusivity within SFS that differ with regards to their targeted career stages, approaches, and successes; and 4) provide suggestions for how SFS and individual members can continue to expand these efforts. The goal is to initiate a call to action for SFS and its members to actively think about and improve diversity, equity, and inclusivity in our scientific society.

In addition to examining who is doing freshwater science, I examine how humans are altering freshwater ecosystems. Humans have altered two-thirds of the world's rivers so that they are no longer free-flowing (Grill et al. 2019). Thus, they face unique biodiversity threats, particularly from hydropower dams (Nilsson et al. 2005; Winemiller et al. 2016). In the U.S. alone, there are >2,500 hydropower dams that impact biodiversity across river basins (Stanford and Ward 2001; Hadjerioua et al. 2012). Large hydropower dams change the physical nature of a river by creating barriers to dispersal and altering dissolved oxygen levels, nutrients, temperature, suspended sediment loads, and flow regimes (Friedl and Wüest 2002; Graf 2006; Tortajada et al. 2012). Altered flow regimes are of particular interest due to the critical role of flow in dictating ecological and evolutionary processes (Poff et al. 1997; Bunn and Arthington 2002; Lytle and Poff 2004). Hydropower dams can either reduce or amplify variation in flow, depending on the timescale being examined. On the seasonal or annual scale, homogenization of flow occurs through reduction of seasonal flow extremes, but on a daily basis, fluctuations between high and low flows can be amplified to meet sub-daily changes in electricity demand, a procedure known as hydropeaking (Poff et al. 2007; Førsund 2015). Thus, organisms occupying tailwater habitats downstream of hydropower dams can be subject to both decreased flow variability at seasonal timescales and increased flow variability at daily timescales (Moog 1993). These flow alterations may exclude invertebrate taxa with complex life cycles, such as those with both aquatic and terrestrial stages, thus impacting ecosystem processes by limiting energy transfer from aquatic to riparian ecosystems (Kennedy et al. 2016; Ruhi et al. 2018). With the large and increasing number of hydropower dams globally (Zarfl et al. 2014) and the wide variation in biological responses seen across regions (Poff and Zimmerman 2010), there is a need to assess how damming and flow management within entire river basins impacts biodiversity at both the local scale downstream of a single dam and at the regional scale across entire river basins.

In Chapter 3, I quantify invertebrate dominance, richness, abundance, and biomass at multiple sites within the tailwaters downstream of seven major Colorado River Basin dams that span a range of hydropeaking intensities. Specifically, I determine (1) whether hydropower dams influence patterns of invertebrate dominance and community structure, (2) whether hydropeaking intensity affects the proportion of insect and EPT taxa, and (3) how dominance, richness, abundance, and biomass change with increasing distance from dams. I predicted that within each tailwater and across the Colorado River Basin a few highly abundant non-insect taxa would dominate invertebrate communities. I also predicted that hydropeaking intensity would disfavor taxa with complex life cycles, thereby reducing the proportion of insect and EPT taxa in terms of richness, abundance, and biomass. Finally, due to attenuation of dam impacts with distance downstream, I predicted that distance downstream of a dam would be inversely related to dominance of the full invertebrate community and positively related to local richness, abundance, and biomass.

In Chapter 4, I focus in on one hydropeaking dam, Glen Canyon Dam and the ecosystem downstream, the Grand Canyon, to examine how molecular data can provide insight into the movements of aquatic insects and potential dam impacts within a fragmented landscape. Landscapes are naturally fragmented, and humans have exaggerated this fragmentation, negatively impacting how many species disperse (Haddad et al. 2015). Both natural and anthropogenic fragmentation are present in the Grand Canyon, a deep canyon (average of 1600 m) located in a harsh desert ecosystem. This river system is highly modified by hydropeaking (i.e., daily flow fluctuations associated with hydropower generation) from Glen Canyon Dam, which render the mainstem uninhabitable for most insect species, potentially creating a dispersal barrier (Kennedy et al. 2016). Many aquatic insects have a complex life cycle with an aquatic juvenile followed by an aerial adult life cycle, which enables dispersal to happen along several avenues (Downes & Reich 2008). Juveniles can actively crawl or swim upstream or passively float downstream, and adults can actively fly to new habitats or passively disperse on wind currents. The success of a species to utilize particular dispersal methods is dependent on both the physical characteristics of a species, i.e., body size and wing length, as well as the surrounding environmental conditions (Poff 1997). To explore the intersection of natural and human induced landscape fragmentation, I quantified caddisfly, mayfly, and water strider population structure throughout the Grand Canyon. I predicted (H1) the relationship between a species' genetic distance and geographic distance will be mediated by adult dispersal ability. Specifically, I predict that species with low adult dispersal ability (in this study, a water strider), will be most influenced by genetic drift; species with moderate dispersal ability (a mayfly) will show isolation by distance (IBD), and species with high dispersal ability (a caddisfly) will be most influenced by gene flow. I predict (H2) for species most influenced by IBD that Euclidian distance will be a better predictor than river network distance, and that species most influenced by genetic drift and gene flow will show no influence of geographic distance on genetic differentiation.

I conclude this dissertation with a chapter (Chapter 5) summarizing my main findings from each chapter and an overall call to action for my readers. I do not think it can be repeated enough: humans have always lived and will continue to live in perilous, but hopeful times. It is incumbent upon us to address the major challenges of our time (which I perceive as COVID-19, racial inequity, and climate change) and to work towards creating a more just, equitable, sustainable, and loving society. This work is a burden that humans must forever carry, but we can carry it joyfully, with hope, and by celebrating the achievements that we are able to make along this path.

Chapter 2 – Diverse, equitable, and inclusive scientific societies: Progress and opportunities in the Society for Freshwater Science

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2.1 Abstract

Discussions about diversity, equity, and inclusivity are becoming increasingly common in scientific societies. However, more concerted efforts are needed to recognize and challenge systemic discrimination to ensure scientists from marginalized groups can contribute to and benefit from scientific societies. Here, we evaluate efforts and opportunities within the Society for Freshwater Science (SFS) as examples for how scientific societies can make progress toward diversity, equity, and inclusivity. In 2017, SFS collected anonymous demographic information and open-ended feedback from SFS members through an online survey. We combined this information with 2 examples of recent initiatives and challenges that occurred within SFS. We present a guide for SFS and other scientific societies toward creating a more welcoming and equitable space for all scientists. To prioritize diversity, equity, and inclusivity, scientific societies must center the voices of marginalized and underrepresented people in all scientific society activities, including within groups of all sizes and at all society events. These actions will allow scientific societies to better represent and engage with their current and future members and the broader communities those members serve.

2.2 Introduction

For centuries, science has been a nearly-exclusive domain of upper-class white men, with limited opportunities for marginalized people to either make or be recognized for notable scientific contributions (Bronstein and Bolnick 2018). Marginalized people are discriminated against or oppressed based on characteristics such as race and ethnicity, class, religion, national origin, language, citizenship, marital status, sex, age, differing abilities, sexual orientation, gender identity and expression, transgender status, and parental or pregnancy status. Although science participation has broadened over the last several decades, most American scientific societies remain disproportionately white, male, heterosexual, and cisgender (George et al. 2001, Stevens et al. 2008, Beck et al. 2014, Arismendi and Penaluna 2016, Penaluna et al. 2017). Furthermore, many major scientific awards, positions of leadership within societies, and invited speakers and panels at major scientific conferences lack representation from marginalized groups (Schroeder et al. 2013, Sardelis and Drew 2016, Silver et al. 2017).

Many scientific institutions still fail to adequately address the ways that societal systems of privilege and power operate to marginalize members of our communities (Brown et al. 2017, Potvin et al. 2018), although most institutions now recognize that broadening participation and increasing diversity are important goals. Discrimination can take multiple interacting forms, depending on a person’s identities (e.g., race, gender, class, culture, and professional status). We define terms, such as identity, based on their usage in current discourse of diversity, equity, and inclusivity in STEM. We acknowledge that the meanings of these terms are fluid and are subject to change as the public conversation progresses (see Figure 2.1 for a glossary of relevant terms). We must consider how discrimination acts on these identity dimensions and question how our current practices and the legacy of past practices may reinforce exclusion and discrimination within our scientific societies. Here, we discuss how the Society for Freshwater Science (SFS) and its members have worked to reduce barriers against diversity, equity, and inclusivity, and we highlight areas where additional progress will further advance this goal. In particular, we: 1) review the function of diversity, equity, and inclusivity in scientific societies; 2) outline the current demographics and cultural climate within SFS; 3) describe 2 examples intended to increase diversity, equity, and inclusivity within SFS that differ with regards to their targeted career stages, approaches, and successes; and 4) provide suggestions for how SFS and individual members can continue to expand these efforts. The goal of this article is to initiate a call to action for SFS and its members to actively think about and improve diversity, equity, and inclusivity in our scientific society.

2.2 Functions of diversity, equity, and inclusivity in scientific societies

Increasing diversity, equity, and inclusivity in science and scientific societies has 2 main functions: to promote scientific advancement and to fulfill a moral and ethical obligation to our peers. We define diversity as the variety of identities present, equity as providing people with what they need to be equally successful, and inclusivity as supporting a collaborative environment that values diversity and equity (Figure 2.1). Scientific societies function to bring together people working on related topics, thereby facilitating networking and career development and shaping the direction, culture, and ethics of their fields (Mason et al. 2016). In addition, scientific societies advance scientific knowledge, facilitate public understanding of science, and engage with policy makers. To accomplish this goal of scientific advancement, many scientific societies recognize that greater membership diversity can lead to better science by broadening viewpoints, questions, and problem-solving skills (Nathan and Lee 2013, Page and Vandermeer 2013, Lee 2015, Trax et al. 2015, Gao and Zhang 2016, Nielsen et al. 2017). For example, the SFS Statement on Diversity, approved in June 2016 (Figure 2.2, Figure 2.3), contextualizes the value of diversity as a belief that it “fosters a richer understanding of freshwater ecosystems and conservation of global freshwater resources”. The benefits of diversity will not be realized, however, unless scientific societies work to increase equity and inclusivity by welcoming and valuing members of marginalized groups and removing barriers to their participation (Joshi and Roh 2009, Maton et al. 2016, Puritty et al. 2017).

By increasing diversity, equity, and inclusivity, society members fulfill a moral and ethical responsibility to include everyone in scientific spaces and serve populations affected by the issues we study here. To work toward a more equitable scientific enterprise, we must examine whom the society is serving, both directly and indirectly, and the ways that cognitive and structural biases influence our activities. For example, although SFS has a stated mission to increase diversity and inclusivity within its membership (Figure 2.2), the current SFS mission statement does not include social justice issues related to freshwater resources. If diversity, equity, and inclusivity are goals for SFS, we must expand our focus to include the populations affected by the issues we study, including how reduced water quality and quantity, unequal access to clean water, and diminished ecosystem services disproportionately harm poor and otherwise marginalized communities (Balazs et al. 2012, Hanna-Attisha et al. 2016, McIntyre et al. 2016, Brooks et al. 2017, Switzer and Teodoro 2017). Our research, as well as our professional societies, must include the voices and participation of marginalized people to fulfill our moral and ethical obligations.

Several scientific societies have begun to assess their demographics and provide frameworks for actively encouraging diversity, equity, and inclusivity (e.g., Penaluna et al. 2017). However, a number of additional activities may be necessary to successfully counter systemic oppression and implement these frameworks. These activities include: amplifying marginalized voices; recognizing and validating different cultures and experiences; ensuring leadership positions, opportunities, and awards are received by members from diverse groups; providing financial and material support for members who have fewer resources; and addressing systemic societal and implicit biases. Continuing to reform institutions and their practices will strengthen our science and help to fulfill our moral and ethical obligations (Ely and Thomas 2001, Nielsen et al. 2017).

2.3 Approaches to diversity, equity, and inclusivity within scientific societies

We identify 3 general approaches that scientific societies can take to increase diversity, equity, and inclusivity. First, the traditional approach has been to assume that science is innately a value-neutral, colorblind process of knowledge creation that cannot discriminate. Thus, scientific organizations need only to focus on the science. However, this view privileges the majority and perpetuates oppression toward other groups by ignoring the different barriers that people with marginalized identities face in doing science (Pless and Maak 2004). In addition, this approach forces marginalized members to assimilate into the dominating culture without recognizing their own unique experiences (Shore et al. 2011).

A 2nd approach recognizes that science has a diversity problem and works to celebrate diversity and enact anti-discriminatory policies (e.g., societal codes of conduct) (Adamo 2013, Massey 2015, Kaplan et al. 2018). These activities are becoming mainstream among scientific societies (e.g., Penaluna et al. 2017), yet significant social, cultural, and institutional barriers remain and continue to marginalize people (Haynes and

Jacobson 2015, McGlynn 2017, Potvin et al. 2018). Even when scientific society members and leadership recognize the value and moral imperative of increasing diversity in our fields, scientific societies still lack mechanisms to ensure equitable and inclusive environments. Societies can actually cause greater harm by recruiting marginalized scientists into discriminatory and exclusionary environments (Puritty et al. 2017). Diversity, equity, and inclusivity are a 3-legged stool. Focusing solely on diversity and ignoring inclusivity and equity can backfire by bringing marginalized groups into environments where they are then excluded and do not receive adequate support to succeed.

A 3rd approach is to actively advance diversity, equity, and inclusivity through the lens of social justice with continuous work to combat systematic bias. Scientific societies can enact policies and programs that explicitly and proactively include and amplify the viewpoints of people with marginalized identities and provide them financial and material support. This approach, for which we advocate, requires a concerted effort by scientific society leadership and fellow members to counteract the unconscious biases and intentional social forces (e.g., racism, sexism, xenophobia, homophobia, ableism, colonialism) that cause systemic discrimination (Roberson 2006, Prescod-Weinstein 2017). Unlike the first 2 approaches, this approach ensures that the environment into which marginalized scientists are being recruited is one that recognizes and supports their experiences while simultaneously creating a culture of belonging (Shore et al. 2011). The discourse and role of scientific societies can evolve over time toward this 3rd approach through the concerted efforts of advocates and the official adoption of progressive policies and practices (Figure 2.3). In the following sections, we detail SFS demographics and culture and describe approaches that SFS has used to advance diversity, equity, and inclusivity.

2.4 Status of diversity, equity, and inclusivity in SFS: Membership survey

In May 2017, SFS e-mailed out its 1st demographic survey, which included questions concerning members' attitudes toward diversity, equity, and inclusivity. This survey was created by an SFS ad-hoc committee on inclusivity and e-mailed to all members enrolled in SFS at any time from 2014 to 2017. The creation of this committee and the survey were prompted by concerns over the 2017 SFS annual meeting held in Raleigh, North Carolina following the passage of the state's House Bill 2. This House Bill, passed in 2016, eliminated city- and county-level anti-discrimination protections for lesbian, gay, bisexual, transgender, and queer (LGBTQ+) individuals, including removing protections for transgender and gender non-conforming individuals to use public restrooms based on their gender identity (Figure 2.3). We acknowledge that some of the responses to the survey may have been influenced by this context.

Once e-mailed, the anonymous online survey remained open for 10 d prior to the SFS annual meeting in June 2017. We received 279 responses, which represented ~20% of the 1426 registered SFS members at that time. Two-thirds (66%) of respondents were under age 50, and ½ of respondents had been members of SFS for >10 y. Most respondents were United States (US) residents (84%) and worked in academia (70%), particularly at doctorate-granting universities (Table 2.1). Eleven respondents were from Hispanic-Serving Institutions, none were from Historically Black Colleges and Universities or Tribal Colleges and Universities, and 5 were from institutions that have over 25% African American undergraduate enrollment. Respondents overwhelmingly identified as white (87%). Like other ecology-centered scientific societies, SFS has a higher proportion of white members than the US population as a whole, US college students, or full-time faculty at US colleges (Table 2.2). Women, respondents with disabilities, and individuals from marginalized racial backgrounds were underrepresented in SFS relative to the US population (Figure 2.4). Only 0.7% of SFS survey respondents identified as Black, although African Americans represented 6% of the US professoriate in 2015. Similar underrepresentation of people identifying as Black exists in other professional societies representing the aquatic or ecological sciences, including the Ecological Society of America (1%; Beck et al. 2014) and the American Fisheries Society (1%; Penaluna et al. 2017). We chose to compare SFS demographics to the US population, US college students, and US faculty (Table 2.2) as most SFS survey respondents were US residents and worked in academia. We present these comparisons, in addition to data on other professional societies, to highlight the opportunity that SFS has to recruit people with marginalized identities and how other scientific societies compare.

People who identified as transgender and people who identified as LGBTQ+ constituted a higher percentage of survey respondents than those identifying as such among US adults (Figure 2.4; Flores et al. 2016, Newport 2018). This result has 2 possible explanations. First, LGBTQ+ members may have responded to the survey at higher rates than members who do not identify as LGBTQ+, possibly motivated by events leading up to the 2017 SFS meeting (Figure 2.3). Second, SFS may have a relatively-large LGBTQ+ population. In either case, SFS would benefit from recognizing and celebrating this diversity as well as fostering inclusivity by actively working to serve and retain these members. Undergraduates who are LGBTQ+ have a 7% lower retention rate in science, technology, engineering, and math (STEM) fields relative to heterosexual, cisgender undergraduates (Hughes 2018), which highlights the opportunity SFS has to contribute to improving STEM retention.

The survey also asked respondents about barriers to attending the SFS annual meeting. Responses suggest that decisions about meeting locations may contribute to lower attendance rates for LGBTQ+ individuals. In fact, of the 50% of respondents who did not plan to attend the 2017 meeting because of travel and registration costs, 20% also identified the North Carolina House Bill 2 as a barrier to attendance. Additionally, the survey demonstrated that those who identify as LGBTQ+ were affected more by barriers to attending the 2017 meeting than were non-LGBTQ+ identifying members (n = 79; p = 0.003, χ^2 = 11.45, df = 2). Furthermore, several states withheld funding for travel to North Carolina because of House Bill 2, and these funding restrictions affected many state-funded SFS members. This situation is not unique to North Carolina. At the time of this writing, there are 11 states to which California has banned state-funded and state-sponsored travel because these states have enacted laws that require or allow discrimination on the basis of sexual orientation, gender identity, or gender expression.

Responses from the survey highlighted a possible gap between the intention to be an ally to LGBTQ+ members in SFS and meaningful action to demonstrate allyship (i.e., the process of building relationships based on trust and accountability with marginalized people). Only 11% of respondents had taken formal inclusivity training, such as ally or safe zone training, although 73% of respondents considered themselves LGBTQ+ allies.

Although formal training is not required to be an ally, nor does it ensure allyship, it does show that a person is taking meaningful action. Demonstrating true allyship is necessary for the retention of scientific society members with marginalized identities. Retention of LGBTQ+ individuals is higher than retention of individuals from some other marginalized groups in STEM, such as African American and Latinx students (Hill et al. 2016), but it remains lower than that of privileged groups, such as white, cisgender, heterosexual males (Hughes 2018).

The survey concluded with 3 open-ended questions, allowing respondents to suggest ways to increase inclusivity and accessibility and share their thoughts on the status of diversity, equity, and inclusivity within SFS (see Table 2.3 for specific questions). To quantify these results, we coded SFS member responses to these questions as positive (in support of additional actions and attentions by SFS to improve diversity, equity, and inclusivity); neutral (no preference or unsure); or negative (not in support of further action to increase diversity, equity, and inclusivity in SFS). The answers were independently reviewed by 3 people to ensure consistent coding. To avoid bias, the reviewers were not given the demographic information associated with written answers. Corresponding demographic information was attached to the written answers post-coding for further analysis. Most responses to all 3 questions were positive, but we did receive some negative responses as well. The greatest percentage of negative comments were in response to the question about LGBTQ+ inclusion (15%) followed by the question about general diversity, equity, and inclusivity efforts (14%). Negative responses to the question about inclusion of people with disabilities constituted only 1% of total responses (Table 2.3). The negative responses to diversity questions were largely from people who identified as white men, although some white women also responded negatively. None of the respondents who submitted negative responses identified as LGBTQ+, and only 1 identified as having a physical disability. Other respondents who responded negatively chose not to provide demographic information. The negative responses received in this survey underscore the need for the demographic majority members of SFS and other scientific societies to engage in opportunities to interact with and learn from those with marginalized identities. Creating a conference environment where diversity, equity, and inclusivity efforts are treated as seriously as scientific research can help to increase participation of marginalized groups in science (Leung 2018).

Finally, this survey is the 1st broad demographic survey of SFS membership that can be used to follow and challenge our progress into the future. We encourage future surveys of SFS membership to continue to track both demographics and attitudes toward inclusivity and equity of our scientific society. Our survey focused more on LGBTQ+ demographics, given the issues surrounding the location of the 2017 SFS annual meeting, but more survey efforts are needed to identify demographic make-up and potential barriers to inclusion across other marginalized groups. Importantly, marginalized racial groups, women, and respondents with a disability were not well represented in this survey effort and are not well represented in SFS.

2.5 SFS efforts to increase diversity, equity, and inclusivity

The 2017 survey was meant to formally gauge the state of the society in terms of current thoughts and perspectives on diversity, equity, and inclusivity. The survey highlighted the need for increased diversity, equity, and inclusivity within SFS, and here we discuss 2 examples of SFS and its members doing this work. The 1st example is the Instars mentoring program, a long-term initiative by SFS that has increased recruitment and retention of students from marginalized groups. The 2nd example is the North Carolina House Bill 2 coupled with the 2017 SFS meeting in Raleigh, which demonstrates the work that remains to be done for SFS to be inclusive along multiple identity dimensions.

2.5.1 Instars mentoring program

SFS has actively invested in efforts to broaden diversity within its membership by sponsoring undergraduate students from underrepresented groups (i.e., those who identify as either being from a marginalized racial group, being a 1st-generation student, or having a disability) to attend the SFS annual meeting as Instars Fellows through the Instars mentoring program. Before the start of the meeting, Instars Fellows take part in a half-day orientation workshop to learn the layout of a typical scientific meeting, and a group of graduate student mentors help the Instars Fellows navigate the meeting. During the meeting, Instars Fellows attend plenary sessions and a variety of special, technical, and poster sessions. They are guided through multiple networking activities, participate in a professional development workshop, and have opportunities to present their own research.

A large part of the program's success is attributable to the financial buy-in and recruitment support from SFS leadership and membership at large. Specifically, the program currently operates as a line item in the annual meeting's budget. Three other main factors also contribute to the program's success. First, there is involvement from many junior and senior SFS members, as a rotating advisory group who review student applications and provide feedback on funding allocations. Second, the Instars program offers targeted undergraduate sessions involving well-established scientists who engage with Instars Fellows at meet-and-greet activities associated with the meeting's special presentation session on education. Third, Instars enlarged the graduate mentoring program by enlisting the assistance of the Student Resources Committee. This committee is composed of graduate and undergraduate students who participate in fundraising and organizing activities to enhance the sense of community within SFS. As a result of Instars activities, some past graduate mentors are now active members in the SFS Education and Diversity Committee, which oversees the program. Another important measure of the program's success is the number of past fellows who have maintained SFS membership and have returned to the annual meeting and participated in the program as graduate mentors (Figure 2.5B).

The SFS Instars mentoring program has funded an average of 14 fellows annually by providing a stipend (~$635/student, though this amount varies by year and meeting location) and also covering meeting registration costs, as well as some meals and activities, to supplement the cost of attending the annual meeting (Figure 2.5C). In 2011, the inaugural year of Instars, SFS allocated $900 to the program, which partially funded the meeting expenses of 6 fellows. Since 2011, SFS has allocated more than $80,000 (~$10,000/y; Figure 2.5A) for program activities to continue the Instars mission of "recruiting students from under-represented groups to freshwater science, particularly as pursued by the academic diversity of SFS scientists". As of the 2019 SFS meeting, SFS Instars has been approved for funding for the next 3 y with an annual budget of $15,000. SFS's investment is extended by funds available through some of the students' home institutions and grants to the students' advisors. Note that the Instars advisory group and graduate mentors volunteer their time at no cost to SFS.

A recent survey of past participants in Instars (*n* = 40 respondents; 40% of total past participants at time of survey) showed that 35% of Instars Fellows are current SFS members. More than 37% have attended a scientific society meeting after participating as fellows, with 15% having attended 3 to 5 additional meetings. More than 95% of survey respondents indicated they had become more aware of educational or career opportunities in freshwater science and ecology, as well as having become more aware of environmental issues, because of their participation in the program. Furthermore, 95% of survey respondents indicated that their confidence in their ability to excel in a STEM field increased after participating in Instars. A similar percentage credited their participation in the program as having a positive influence on their decision to pursue graduate studies and a career in a related field. Additionally, more than 80% of survey respondents indicated that their perceptions of the types of people who pursue careers in freshwater science, ecology, or environmental science had changed in a positive manner after participating in Instars. Survey respondents also reported that their impression of the openness and inclusiveness of freshwater science, ecology, or environmental science had positively changed after their involvement in the program. All survey respondents indicated that their interactions with other program participants and meeting attendees were overwhelmingly positive and beneficial. Nearly ½ of survey respondents (48%) remain active in freshwater science, 80% remain involved in ecology or environmental science, and all respondents reported active involvement in a STEM field. The vast majority of survey respondents (>90%) indicated they continued conducting scientific research following their participation in Instars. More than 15 previous fellows have completed or are presently in graduate programs in freshwater science or a related field.

The Instars mentoring program is an excellent example of a grassroots membership organizing effort that received financial support from SFS leadership and created a successful program to increase diversity, equity, and inclusivity within SFS at the undergraduate level. Other scientific societies have adopted comparable diversity initiatives with active programming, with varying levels of financial support and subsequent reporting on participant retention and success. For example, since 1996, the Ecological Society of America (ESA) has maintained a student mentoring program known as the Strategies for Ecology Education, Diversity, and Sustainability (SEEDS; Mourad et al. 2018). The SEEDS initiative is substantially larger than SFS Instars, with an annual budget of >$300,000 and several full-time staff running the program. However, SEEDS has resulted in retention metrics similar to SFS Instars, with 47% of program participants subsequently pursuing graduate programs in ecology and 23% of survey respondents remaining members of ESA. Survey responses from SEEDS and SFS Instars indicate that ongoing, maintained efforts to increase scientific society diversity result in overall positive outcomes. Our demographic survey from 2017 also suggests that Instars has succeeded in increasing diversity, equity, and inclusivity at the undergraduate level. However, more work is needed to propagate these successes into later career stages and across other marginalized identity dimensions.

2.5.2 SFS annual meeting inclusivity plan

The Instars mentoring program is an example of successful efforts to advance diversity, equity, and inclusivity; however, the 2017 SFS meeting in Raleigh, highlights the work we still must do as a scientific society. In 2016, the SFS Elections and Place Committee recognized the issue of North Carolina House Bill 2 but decided against moving the annual meeting because financial commitments for the meeting had been made prior to the bill's passage. Having made the decision, SFS released several statements avowing support for LGBTQ+ members and promising that actions would be taken to ensure an inclusive meeting. However, members questioned the decision not to change the location once it became clear that some SFS members would be unable to attend, would feel unsafe attending, would not receive funding to attend, or wished to support the international economic boycott targeting North Carolina over House Bill 2. Concurrent with the 2017 SFS survey described above, an ad-hoc committee, composed of affected members and allies, formed through grassroots organizing and made recommendations to the Annual Meeting Committee regarding opportunities to make the meeting more inclusive. Some, but not all, of these recommendations were accepted in a statement posted as the 2017 SFS Inclusivity Plan on the meeting webpage (https://sfsannualmeeting.org/archive/2017/InclusivityPlan.cfm). In this plan, SFS pledged to provide a safe and inclusive environment to all attendees; raise awareness across the broad membership; provide remote access to plenary talks and promote social media discussions for those unable to attend the meeting; and increase formal institutional support of inclusivity within SFS. Nevertheless, survey results showed that

LGBTQ+ members disproportionately considered House Bill 2 a barrier to attending the annual meeting.

As the ad-hoc committee on inclusivity worked with the SFS Executive Committee and the 2017 Annual Meeting Committee, it was clear that the intention of the committees was not to produce feelings of exclusion. Instead, issues arose because members directly harmed by the House Bill 2 were not included in meeting planning and subsequent related decisions. We emphasize that—as both the Annual Meeting Committee and the ad-hoc committee on inclusivity had hoped—many positive steps were taken at the 2017 meeting to increase inclusivity. For instance, the meeting featured a place for people to indicate their pronouns on name badges, gender-neutral bathrooms at the conference center and hotel, and a map of LGBTQ+-friendly businesses with gender-neutral bathrooms in the surrounding area. Presentations by ad-hoc committee members about inclusivity and diversity during the meeting's opening plenaries raised awareness among members who did not understand the issue of House Bill 2 in North Carolina. For example, a video of testimonials on the benefits of diversity, equity, and inclusivity in STEM was posted to YouTube and shown during the opening plenary (https://www.youtube.com/watch?v=GKXrhSvhsos).

The meeting's commitment to diversity and inclusivity continued beyond the opening sessions. A 4-h workshop, "LGBTQ+ identity and contemporary cultural climate", and a lunchtime workshop, "Understanding gender and sexuality", were organized by Dr Kate Boersma, a member of the SFS ad-hoc committee on inclusivity, in collaboration with the North Carolina State University Gay, Lesbian, Bisexual, and Transgender Center. A number of SFS members who had no prior involvement in the ad-hoc committee attended the meeting’s LGBTQ+ inclusivity workshops and learned how to make their lab groups and classrooms more inclusive. Several students who were unaware of the complex history leading up to these workshops have since remarked to members of the committee how impressed they were by the commitment of SFS to openly discuss these issues. Together, all of these initiatives helped make the 2017 meeting more inclusive for transgender and gender-nonconforming members. Furthermore, to our knowledge, no discriminatory incidents were reported at the meeting.

The efforts made at the 2017 meeting were positive steps toward improving our scientific society as a whole, but work toward a more diverse, equitable, and inclusive scientific society must be ongoing and institutionalized within the culture of SFS. As SFS membership becomes more diverse at lower levels of our organizational hierarchy, we face a new challenge to ensure that these voices are both heard and supported to foster an inclusive organization (Beck et al. 2014, Pezzoni et al. 2016, Smith-Doerr et al. 2017). The decision not to move the 2017 SFS meeting from North Carolina serves as an example of how SFS leadership (i.e., the Board of Directors) could have sought the perspectives of marginalized (in this case, LGBTQ+) members in the decision-making process from the start. In addition, the 2017 meeting is an example of scientific society leadership and members responding to enact change after inclusivity issues arose. This example focuses on LGBTQ+ identities, but other marginalized identities (e.g., parental status, ability status, socioeconomic status, citizenship status) face financial and logistical barriers to meeting attendance and participation. A plan for increasing inclusivity and equity in meeting attendance and participation should consider these and other identities.

2.6 What has happened since the 2017 SFS meeting?

After the Raleigh meeting catalyzed greater attention to diversity, equity, and inclusivity, SFS has continued to become more inclusive by supporting changes implemented in 2017 and through additional equity and inclusivity measures at meetings and within SFS institutional structure (Figure 2.3). In 2018, the SFS Board of Directors approved an updated meeting Code of Conduct with repercussions for individuals who violate its terms and a clear mechanism for reporting violations (https://freshwater-science.org/about/society-governance/code-of-conduct). Several members of the 2017 ad-hoc committee led the organization of and fundraising for the 1st official Diversity and Inclusivity Mixer at the 2018 meeting, which was inspired by an unofficial and impromptu LGBTQ+ mixer at the 2017 meeting. The Diversity and Inclusivity Mixer was intended to expand upon the LGBTQ+ mixer to also include meeting attendees who are marginalized on other identity dimensions. Private fundraising efforts generated over $1000, which was matched by SFS presidential discretionary funds. The 2018 mixer was attended by 75 to 100 SFS meeting attendees, many of whom were students and early career members. With financial support from the Board of Directors, this mixer is slated to become a regular part of annual meetings.

Members of the Elections and Place Committee have indicated that they are more actively thinking about which locations could pose barriers to attendance as well as creative solutions in the event that laws like House Bill 2 affect future meetings. Additionally, at the 2019 meeting, a local tribal chairman gave a territorial acknowledgement. This statement provided awareness of local Indigenous presence and land rights and highlighted the importance of recognizing our history of colonialism and a need for change in settler-colonial societies. Furthermore, the Education and Diversity Committee has been given a voting seat on the Board of Directors, which will allow more diverse voices to have a say in future SFS policies and decisions. These steps all represent progress toward increasing and retaining diversity in our membership.

To conclude, we offer our suggestions for continued improvement in diversity, equity, and inclusivity within SFS. These suggestions are intended to be a starting point for further conversations about strategies for advancing diversity, equity, and inclusivity within SFS and other scientific societies, who may also find many of these suggestions helpful. Additionally, we encourage SFS to solicit suggestions from the entire community on how to make SFS more diverse, equitable, and inclusive.

2.7 Suggestions for SFS future work on diversity, equity, and inclusivity

Increasing diversity and creating inclusive spaces requires change at all levels of organizational hierarchy. We offer our suggestions for how to move forward as individuals, research groups, institutions, and scientific societies but note that action at all levels still requires action by individual members. We provide an additional list of resources in Appendix A as a potential starting point, and we encourage readers to seek out additional material as they continue working toward understanding privilege, equity, and inclusivity.

2.7.1 Individual level

Educate yourself Learn about and trust the lived experiences of people with different identities who experience discrimination and exclusion. Avoid only asking others to educate you. Instead, seek out available resources to educate yourself (e.g., follow people on social media and other platforms who discuss these issues).

Take time for self-exploration Set aside time to reflect upon your own social identity (e.g., gender, race and ethnicity, class, ability, professional title) and consider how the various aspects of your identity may benefit you in scientific, professional, and public spaces. Those in the demographic majority often feel that their identity is normal. However, this feeling of normality usually comes from being in a dominant position in society, a position reinforced by media representation and societal norms. Recognize that the privilege that your identity provides you is not necessarily a choice, but what you do with it is your choice. Consider how you can use your privilege to uplift and support others.

2.7.2 Research-group and institution level

Encourage open conversations Enable dialogue about diversity, equity, and inclusivity in your groups and institutions. Be aware of and actively work against power dynamics and internal biases that may limit these conversations. Always promote and trust the voices of marginalized people and their experiences.

Actively recruit and mentor marginalized individuals First, seek out training for yourself and your colleagues on how to be an effective mentor and advocate for people with marginalized identities. Actively recruit potential graduate students, postdocs, and technicians from organizations that support individuals with these identities. The ESA’s

SEEDS program specifically recruited students from Historically Black Colleges and Universities and found that research experience and positive outcomes in the field of ecology were positively correlated with the decision to pursue a career in ecology (Armstrong et al. 2007).

2.7.3 Scientific society level

Increase representation of marginalized members Ensure that members of underrepresented groups are nominated for scientific society awards, are invited to give plenary talks, and are appointed to or invited to serve on SFS committees and related media. Increase the representation of membership diversity in SFS-affiliated media, such as the *Making Waves* podcast, *In the Drift* newsletter, and other digital outlets.

Track trends in the demographics of membership and the cultural climate of the scientific society to gauge how the society is doing at recruiting and retaining a diverse membership. To ensure that efforts continue, reporting requirements should be added to SFS by-laws. Data collection could take the form of an annual survey of membership. For example, upon membership renewal or meeting registration, encourage people to voice concerns about issues in the scientific society and provide feedback on what has worked well, in addition to collecting demographic data. An annual report summarizing these results, diversity and inclusivity efforts, and progress made could be prepared by the Public Information and Publicity Committee and made available to the membership.

Encourage members and leadership to revisit the scientific society's Mission Statement and Strategic Plan to ensure they reflect a holistic understanding of who the society is meant to serve as well as the diversity, equity, and inclusivity goals presented in the Diversity Statement. For example, the research, education, and service work of scientists that influences the management of freshwater resources directly affects everyone in our communities.

Encourage open dialogue between scientific society leadership and membership

Develop an easier way for membership concerns to reach leaders and for leaders to communicate effectively and transparently with members. Leaders can increase communication with members by posting times and locations of Executive Committee and Board of Directors meetings and providing live streaming and recording. Leaders can also provide more frequent e-mail updates on SFS news (e.g., through the *Monthly Splash* newsletter) and open up major decisions for member comments before voting occurs.

Explicitly state in SFS by-laws that member concerns can be brought to the Board of Directors and Executive Committee by the Education and Diversity Committee representative on the Board of Directors or the Executive Director. Create a digital platform by which members can raise inclusivity concerns with these liaisons anonymously or, if desired, directly submit concerns to SFS leaders. Annual funding should also be allocated for the training of these liaisons.

Members may not be aware of the diversity, equity, and inclusivity initiatives that SFS already implements. We encourage the relevant SFS committees to consolidate information about diversity, equity, and inclusivity work and explore alternative forms of communication, such as providing an annual report on efforts and demographics on the SFS website so that members can get involved and provide feedback.

Continue to expand diversity, equity, and inclusivity efforts at the SFS annual meeting

Encourage members to read and commit to following the annual meeting Code of Conduct and report violations (revised and approved by the Board of Directors in April 2018). Require the Education and Diversity Committee to regularly evaluate the Code to ensure that it supports an inclusive and equitable climate. Continue to require acknowledgement of the Code of Conduct as a mandatory step in registering for the annual meeting.

Continue partnering with other freshwater science groups throughout the globe to pursue efforts to be more inclusive to international members of SFS and to make SFS more representative of the global diversity of viewpoints on freshwater science. The 2018 AQUATROP (an international congress focusing on tropical aquatic systems) meeting in Quito, Ecuador, and the upcoming 2021 SFS meeting in Brisbane, Australia, are great examples of such efforts. Partner with other global societies (e.g., our membership in the Consortium of Aquatic Science Societies and their Diversity Joint Venture, which is a partnership between government agencies, universities, non-profit organizations, and scientific societies to increase diversity in the conservation field).

Provide the membership with a transparent understanding of how and when meeting location decisions are made by dedicating a page on the SFS website to this purpose. Formally place equity and inclusivity concerns in the decision-making framework. For example, meetings should not be planned in locations with laws that discriminate against groups of SFS members or have travel bans in effect or proposed, and a plan should be in place for what to do if laws change after a meeting location has been decided. Incorporate the Education and Diversity Committee into annual meeting planning and solicit membership feedback on the decision-making framework to enhance accessibility and inclusivity.

Design and offer workshops on creating an inclusive classroom and scientific society (e.g., “Inclusive and accurate approaches for teaching sex and gender in biology” workshop by Dr Ash Zemenick, Dr Alex Webster, and Sarah Jones at the 2018 annual meeting).

Expand outreach to local non-profit environmental groups, K–12 educators, and colleges and universities that serve marginalized populations, and invite them to participate in the meeting at a discounted or complimentary rate. Invite local freshwater-related groups, with an emphasis on participation of people from marginalized groups.

Invite local Indigenous leaders to commence meetings with a territorial acknowledgement, an overview of the area’s local tribes, and Indigenous connections to and knowledge of local freshwater resources. Offer speaker fees, free meeting attendance, SFS resources, and other forms of compensation for this work.

Promote Instars and other diversity programming Continue to expand the Instars mentoring program. Work with the Development Committee to seek long-term, sustainable funding for Instars to continue supporting and growing the program. Create text for scientific society members to use in the Broader Impacts sections of National Science Foundation grant proposals to increase research funding for Instars mentees.

Encourage SFS members to develop training workshops for Instars mentees (e.g., “The effective use of improv techniques to advance communication and confidence in the scientific community” workshop by Drs Juliana D'Andrilli and Kaleb Heinrich at the 2018 annual meeting).

Invite more diversity-related programming at the annual meetings. For example, invite program officers from the National Science Foundation to talk about the Louis Stokes Alliances for Minority Participation funding program and other initiatives aimed at broadening participation in the sciences. Offer workshops on mentoring and how to find sponsors.

Continue supporting and developing mixers for different groups to create inclusive social spaces at the meetings, such as the Primarily Undergraduate Institution Mixer and the Diversity and Inclusivity Mixer at the 2018 meeting.

2.8 Conclusions

Those who have privileges or are in leadership roles have a responsibility to work actively toward inclusivity, equity, and diversity while prioritizing the needs and voices of those who have been marginalized. Following challenges associated with the 2017 SFS meeting in Raleigh, North Carolina, and efforts made during the 2018 SFS meeting in Detroit, Michigan, to improve inclusion, we have compiled recommendations on how to create a more inclusive scientific society by listening to the needs of marginalized SFS members. However, the 2 examples of challenges and successes in addressing diversity within SFS described in this paper largely focus on only 2 identity dimensions (race and LGBTQ+ status). Moving forward, it is important for scientific societies and their members to recognize that work on inclusivity must be done across multiple visible and invisible identity dimensions (e.g., parental status, ability status, socioeconomic status, veteran status). From the individual to the scientific society level, we invite every SFS member to participate in actively increasing diversity, equity, and inclusivity within the field of freshwater science. In particular, we challenge individuals from the demographic majority or with privileged identities to commit to breaking down the barriers faced by marginalized scientists. We advocate that this work must continue for the advancement of science and scientists and that the collective effort of all SFS members is needed to make these actions possible.

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Anishinaabe, Peoria, Odawa, Miami, Potawatomi, Anishinabewaki, Sauk/Sac, Tanana Athabaskan, Mohican, Wabanaki, Abenaki, Ohlone, and Yokut peoples.

Cisgender - adjective for a person whose gender identity corresponds with their sex assigned at birth (i.e., someone who does not identify as transgender, gender fluid, gender-nonconforming, gender non-binary, etc.).

Cognitive diversity - a measure of how a collaboration between individuals or groups of different backgrounds, experiences, and perspectives represents a variety of unique identities.

Cultural diversity - the number of unique identities (e.g., ethnicity, race, language, religion, sexual orientation, gender, age/generation, differing abilities, veteran status, immigration status, career status, and intersections thereof) that are present in a group of people.

Equity - providing what individuals need to be successful. Distinguished from equality, which provides exactly the same resources to each individual, regardless of their needs.

Harassment - the act of systematic and/or continued unwanted actions by 1 party or a group.

Identity - the answer to the question, “Who am I?” Identities arise from self-categorization or identification in terms of membership in particular groups, traits, or roles.

Implicit or cognitive bias - attitudes or stereotypes that influence our understanding, actions, and decisions in an unconscious manner.

Inclusivity - the act of supporting a collaborative environment that places value on cultural and cognitive diversity.

Microaggressions - brief and commonplace verbal, behavioral, or environmental indignities, whether intentional or unintentional, that communicate hostile, derogatory, or negative attitudes or reinforce power.

Privilege - unearned advantages derived from identities and attributes of those

Figure 2.1 Definitions of terms used in this paper.

> “The Society for Freshwater Science is dedicated to promoting diversity among its members and welcomes and encourages participation from all, regardless of ethnicity, sexual orientation, gender identity, socioeconomic status, physical or mental difference, religion, age, or national origin. The SFS is inclusive and accepting of all people and built on tolerance, respect, and a welcoming spirit at all of our activities. We strive to actively promote diversity across all levels of our society including members, leaders, committees, and staff. We value a diverse community and believe it fosters a richer understanding of freshwater ecosystems and conservation of global freshwater resources. Members with questions, comments or concerns about SFS diversity issues are encouraged to raise them with a member of the SFS Education and Diversity Committee.”

Figure 2.2 SFS Statement on Diversity. Approved by membership, June 2016.

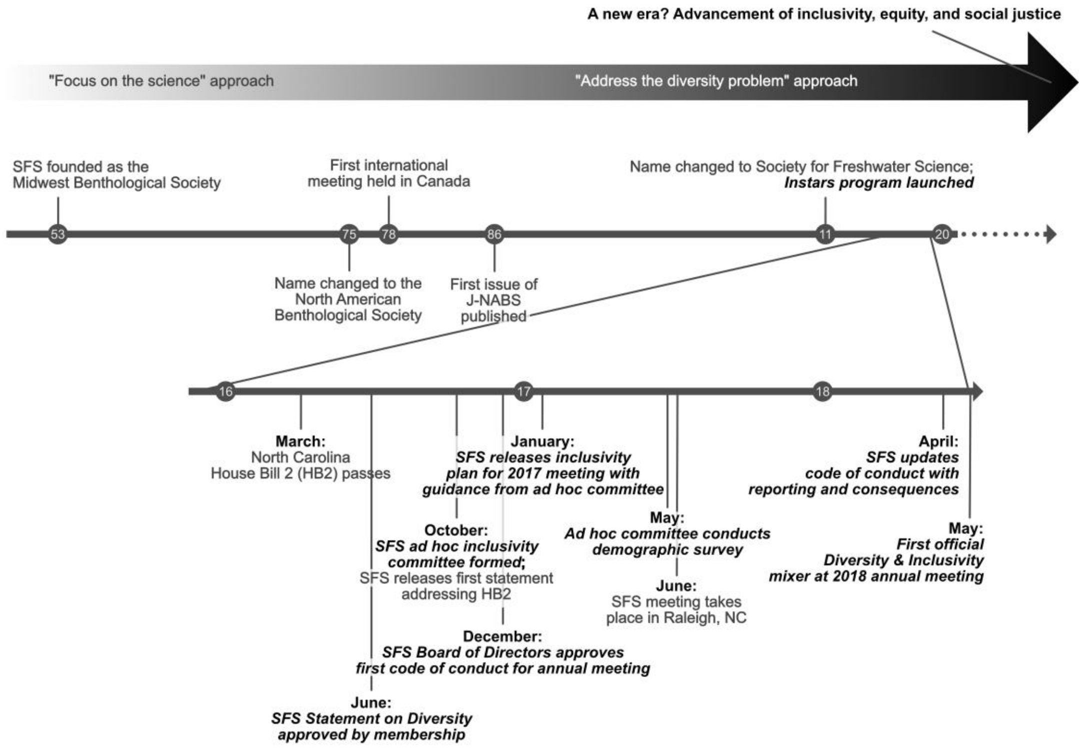

Figure 2.3 Timeline of diversity, equity, and inclusivity activities and events in the context of Society for Freshwater Science (SFS) history. Events of 2016 to 2018 (see text for details) are expanded and highlighted. Top arrow coarsely indicates 3 eras of approaches to increasing diversity, equity, and inclusivity in science. Bolded, italicized text indicates efforts by SFS members and leadership to increase diversity, equity, and inclusivity. Years are abbreviated to 2 digits.

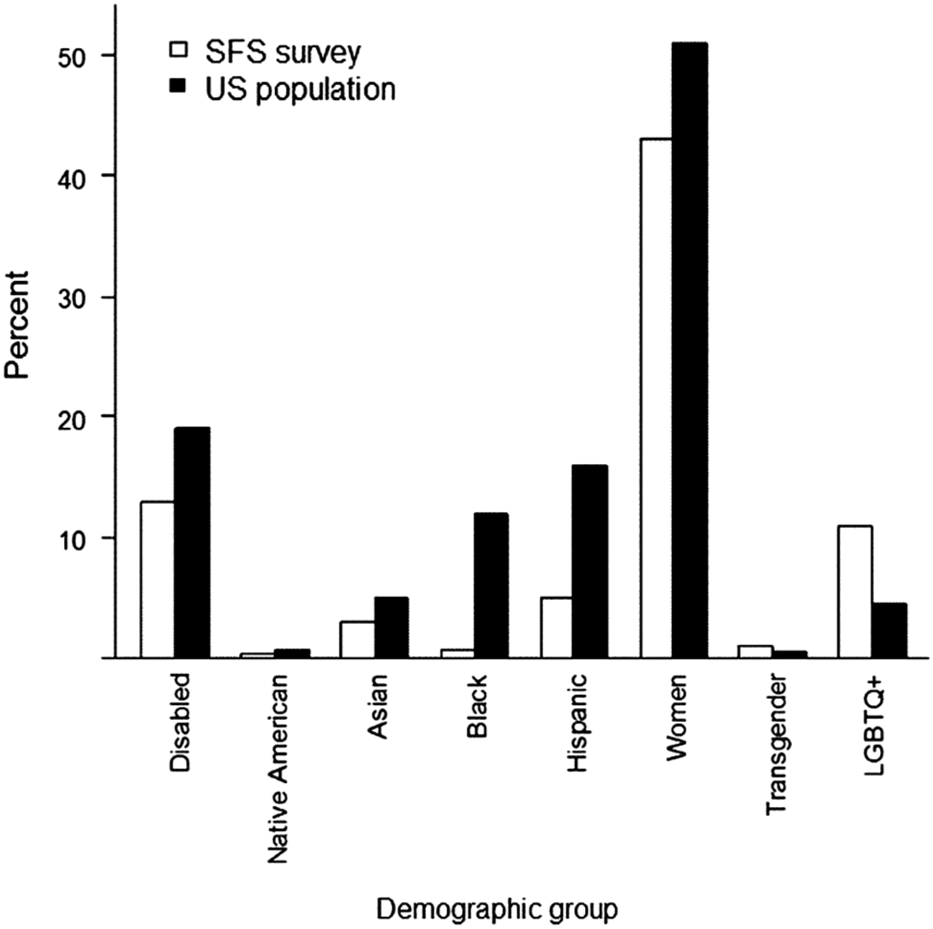

Figure 2.4 Percentage of survey respondents identifying with marginalized groups relative to the United States (US) population. The membership of Society for Freshwater Science (SFS) is international, but we use the US population for comparisons because of the availability of comparable data and because nearly all previous SFS meetings have been held in the US.

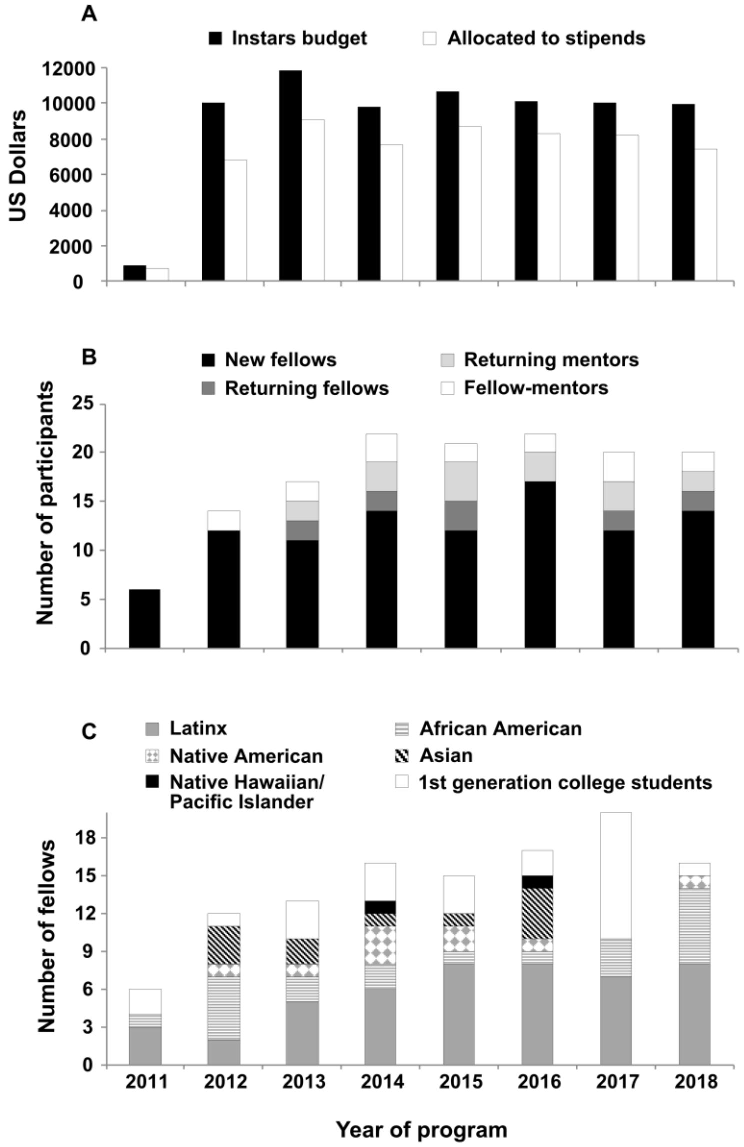

Figure 2.5 Development and current status of the Instars mentoring program. A.—Annual Instars expenditures and amounts allocated to participating student stipends, unadjusted for inflation. On average the program has allocated 78% of the yearly budget to student support to partially cover the cost of attendance to the conference (e.g., registration, travel, lodging, etc.). B.—Instars participation by year (2011–2018), including new undergraduate fellows and students who returned to the program for a 2nd year as undergraduate fellows (returning fellows), graduate mentors (returning mentors), or as undergraduate fellows returning to the program as graduate mentors (fellow-mentors). C.—Number and demographics of students participating in the SFS annual meeting as Instars Fellows from 2011 to 2018. Data provided by Dr Colón-Gaud.

Table 2.1 Summary of the professional affiliation of respondents to the Society for Freshwater Science survey. Percentages for the academia subcategories are based on responses by academics who identified their type of institution. A total of 279 respondents completed the survey.

Position type	% of respondents
Academia	70
Doctorate-granting university	75
Masters-granting university	8
Primarily-undergraduate institution	15
Other	2
Government agency (any level)	17
Private industry	7
Non-profit organization	4
Other	2

Table 2.2 Percentages of different demographic groups present in the United States (US) population: US college students, US college faculty, members of the Ecological Society of America (ESA) and American Fisheries Society (AFS), and respondents to the Society of Freshwater Science (SFS) survey, (reported as all SFS respondents and SFS-student respondents).

Demographic	US population (2010)[a]	US college students (2017)[b]	US college full-time faculty (2015)[c]	ESA (2015)[a] (*n* = 6803)	AFS (2015)[a] (*n* = 3546)	SFS (2017) (*n* = 279)	SFS students (2017) (*n* = 62)
Women	51	56	46	42	25	43	66
Men	49	44	54	58	75	55	34
White	64	58	75	85.5	91.2	87	87
Black	12	15	6	1.3	1	0.7	3
Asian	5	8	10	6.6	3.3	3	3
Latinx/Hispanic	16	17	5	5.3	3.6	5	7
Native American	0.8	unknown	0.5	unknown	0.9	0.4	0
Other[d]	2	2	4	1.3	unknown	3	2

[a] Penaluna et al. 2017.
[b] USCB 2017.
[c] US Department of Education Digest of Education Statistics. (Available from: https://nces.ed.gov/programs/digest/d17/tables/dt17_315.20.asp)
[d] Other includes 2 or more races, prefer not to say, and unknown.

Table 2.3 Number (#) of responses to the open-ended questions on the Society for Freshwater Science (SFS) survey and the percentage of responses coded as positive (i.e., in support of additional actions and attentions by SFS to improve diversity, equity, and inclusivity); neutral (i.e., no preference or unsure); or negative (i.e., not in support of further actions to improve diversity, equity, and inclusivity in SFS).

Question	Total # of responses	% of responses Positive	Neutral	Negative
What can SFS do to make the organization and annual meeting more inclusive to people who are transgender, specifically, and who identify as LGBTQ+, more broadly?	110	74	11	15
What can SFS do to make the organization and annual meeting more accessible to people with disabilities?	67	78	21	1
Please share any thoughts, specific suggestions, or critical feedback on the SFS society and the annual meeting in relation to diversity and inclusivity.	70	86	0	14

Chapter 3 – Hydropeaking intensity and dam proximity limit aquatic invertebrate diversity in the Colorado River Basin

Erin F. Abernethy, Jeffrey D. Muehlbauer, Theodore A. Kennedy, Jonathan D. Tonkin, Richard Van Driesche, and David A. Lytle

3.1 Abstract

River biodiversity is threatened globally by hydropower dams. There is a need to understand how dam management encourages the dominance of certain species while filtering out others. We examined aquatic invertebrate communities within the tailwaters 0-24 km downstream of seven large hydropower dams in the Colorado River Basin of the western United States. We quantified aquatic invertebrate dominance, richness, abundance, and biomass at multiple locations within individual tailwaters and across the basin, and identified biological community effects associated with dam operations and distance from dam. We found that each tailwater was dominated by 3-7 invertebrate taxa that comprised 95% of individuals. Many of these dominant taxa were non-insect, non-flying species and thus were unavailable to terrestrial consumers. Consistent with previous studies, aquatic insects and sensitive EPT taxa (Ephemeroptera, Plecoptera, and Trichoptera) were negatively associated with hydropeaking intensity (magnitude of daily flow fluctuations associated with hydropower generation), which puts limits on the type and perhaps quality of the invertebrate food base. While total invertebrate abundance and biomass did not change with increasing distance from dam, insect and EPT richness, abundance, and biomass all increased, suggesting that impacts of damming are most acute immediately downstream of dams. Our results demonstrate that western U.S. tailwaters can support aquatic invertebrate communities with high abundance, yet low diversity.

3.2 Introduction

Rivers are biodiversity hotspots, but two-thirds of the world's rivers are no longer free-flowing (Grill et al. 2019). Thus, they face unique biodiversity threats, particularly from hydropower dams (Nilsson et al. 2005; Winemiller et al. 2016). In the U.S. alone, there are >2,500 hydropower dams that impact biodiversity across river basins (Stanford and Ward 2001; Hadjerioua et al. 2012). Large hydropower dams change the physical nature of a river by creating barriers to dispersal and altering dissolved oxygen levels, nutrients, temperature, suspended sediment loads, and flow regimes (Friedl and Wüest 2002; Graf 2006; Tortajada et al. 2012). Altered flow regimes are of particular interest due to the critical role of flow in dictating ecological and evolutionary processes (Poff et al. 1997; Bunn and Arthington 2002; Lytle and Poff 2004). Hydropower dams can either reduce or amplify variation in flow, depending on the timescale being examined. On the seasonal or annual scale, homogenization of flow occurs through reduction of seasonal flow extremes, but on a daily basis, fluctuations between high and low flows can be amplified to meet sub-daily changes in electricity demand, a procedure known as hydropeaking (Poff et al. 2007; Førsund 2015). Thus, organisms occupying tailwater habitats downstream of hydropower dams can be subject to both decreased flow variability at seasonal timescales and increased flow variability at daily timescales (Moog 1993). These flow alterations may exclude invertebrate taxa with complex life cycles, such as those with both aquatic and terrestrial stages, thus impacting ecosystem processes by limiting energy transfer from aquatic to riparian ecosystems (Kennedy et al. 2016; Ruhi et al.

2018). With the large and increasing number of hydropower dams globally (Zarfl et al. 2014) and the wide variation in biological responses seen across regions (Poff and Zimmerman 2010), there is a need to assess how damming and flow management within entire river basins impacts biodiversity at both the local scale downstream of a single dam and at the regional scale across entire river basins.

Anthropogenic disturbance, such as hydropeaking from dams, may confer a competitive advantage upon one or a few species, allowing them to displace others and dominate the community (Tilman and Lehman 2001; Seabloom et al. 2003). Downstream of dams, disturbance from daily water stage fluctuations for hydropeaking may favor obligate aquatic taxa that complete their life cycles entirely underwater over terrestrially-available taxa with complex life cycles (i.e., aquatic larval stage and aerial adult stage). For example, Kennedy et al. (2016) showed that the relative abundance of Ephemeroptera, Plecoptera, and Trichoptera (EPT) was negatively related to hydropeaking intensity. Because most EPT taxa lay eggs along the margins of the river, their eggs are subject to daily cycles of desiccation from hydropeaking. In tightly bound canyons where the physical effects of hydropeaking propagate for great distances downstream, the effects of this egg mortality on abundance can be observed for hundreds of kilometers. Thus, by causing a community shift from terrestrially-available to obligatory-aquatic taxa, hydropeaking could have consequences for the amount of biomass available to terrestrial consumers, as well as the diversity of prey available to fish and other aquatic predators.

Local effects of dams may propagate through whole river networks, but the effects are likely greatest in basins with a high density of dams. To understand the effects of dams on basin-wide riverine biodiversity, it is necessary to study biodiversity both locally and across the entire basin (Mac Nally and Quinn 1998; Brosse et al. 2003; Poff and Zimmerman 2010). The Colorado River Basin stretches over seven U.S. states, supplying drinking water to 40 million people, irrigating 5.5 million acres of cropland, and generating approximately 11 gigawatt hours (GWh) of energy annually (Maupin et al. 2018). To serve these purposes the Colorado is one of the most heavily regulated river basins in the world, with 19 large dams (capacity >60,000 megaliters) and >100 smaller dams, many of which are operated for hydropower (Bishop and Porcella 1980; Graf 1985). Thus, this system provides an opportunity to study both local and basin-wide impacts of hydropower dams on biodiversity.

Our study quantified invertebrate dominance, richness, abundance, and biomass at multiple sites within the tailwaters downstream of seven major Colorado River Basin dams that span a range of hydropeaking intensities. Specifically, we sought to determine (1) whether hydropower dams influence patterns of invertebrate dominance and community structure, (2) whether hydropeaking intensity affects the proportion of insect and EPT taxa, and (3) how dominance, richness, abundance, and biomass change with increasing distance from dams. We predicted that within each tailwater and across the Colorado River Basin a few highly abundant non-insect taxa would dominate invertebrate communities. We also predicted that hydropeaking intensity would disfavor taxa with complex life cycles, thereby reducing the proportion of insect and EPT taxa in terms of richness, abundance, and biomass. Finally, due to attenuation of dam impacts with distance downstream, we predicted that distance downstream of a dam would be inversely related to dominance of the full invertebrate community and positively related to local richness, abundance, and biomass.

3.3 Methods

3.3.1 Study sites

We sampled 5–8 sites located from 0–24 km downstream of seven large dams in the Colorado River Basin (Figure 3.1). We use the term "tailwater" to refer to the entire 0–24 km reach sampled downstream of each dam. We calculated hydropeaking intensity for each dam as the mean of the standard deviation of daily flow divided by the mean of daily flow for the five years preceding sample collection (Dibble et al. 2015). The dams were built from 1931–1966 and range in height from 42–221 m. They differ in structure (earthfill, concrete thin-arch, or concrete arch-gravity), primary purpose (hydropower, storage, or flood-control), and reservoir length and capacity (see Table B.1 in Appendix B for more dam-specific information).

3.3.2 Sample collection and processing

Sampling took place during May 2013 (Glen Canyon only) and from May-June 2015 (all other sites). We collected 3–5 replicate benthic samples from the permanently submerged zone at each of the 5–8 sites per tailwater (N = 52 sites). We sampled using the best method for the substrate present. At Fontenelle, Navajo, and Flaming

Gorge Dams where water was wadeable and substrate was predominantly larger gravels and small cobbles, we used Surber sampling. Where water was wadeable and substrates were alternately dominated by finer sediments or larger cobbles, we used Hess sampling and rock scrubbing, respectively (Glen Canyon, Davis, Parker, and Hoover Dams). To sample sand or vegetation substrate in deep water, we used petite Ponar dredge sampling (average depth 4 m, range 1–9m). We determined the area sampled at each site based on the sampling device used or the surface area of the scrubbed rocks, calculated from photos (average sampled area 0.4 m^2, range 0.03–1.4 m^2). We then filtered samples through a 250 µm sieve and stored them in 95% ethanol.

To facilitate processing in the lab, we combined and rinsed the 3–5 replicates from each site before transferring them to a Caton tray sampler for subsampling. We randomly chose a single square of the gridded Caton tray, representing 1/30th of the sample, and removed it from the Caton tray. We then picked all invertebrates from the debris. If the subsample did not yield >500 invertebrates, we repeated the process on another 1/30th subsample, and so on until a count of 500 invertebrates was achieved or the entire sample was picked. Once subsampling was complete, we performed a visual scan of the Caton tray for large-bodied and rare invertebrates missed by subsampling. We identified invertebrates to the lowest feasible taxonomic level, usually genus. We measured the body length of the first 30 individuals and used allometric equations from the published literature to calculate biomass (Benke et al. 1999; Hódar 1996).

3.3.3 Data analysis

To explore whether responses differed across major taxonomic groups, we organized data into three sets: all invertebrates (full data set, including non-insects that do not have a terrestrial phase), insects only (these generally have a complex life cycle with a terrestrial phase), and EPT only (Ephemeroptera, Plecoptera, and Trichoptera, the insect orders considered most sensitive to disturbance; Lenat and Penrose 1996). We calculated richness, abundance, biomass, and dominance for each site. Dominance values for each site were determined from the Simpson index (Simpson 1949) using the *simpson* function in the R software "vegan" package (R Core Team 2016; Oksanen et al. 2019). Simpson's D is a measure of dominance that has a range of $1/R$ to 1, where R is the number of taxa. To characterize invertebrate community structure in different tailwaters, we used the *metaMDS* function in the "vegan" package to create nonmetric multidimensional scaling (NMDS) plots of log-adjusted abundance at the order level (or the lowest taxonomic level above order) with vectors showing the 10 most abundant taxa.

We examined how environmental factors (i.e., distance from dam, hydropeaking intensity, and dam height) affected dominance, richness, abundance, and biomass for all invertebrates, insects only, and EPT only using the *glmmTMB* and *glmmADMB* functions in the R packages of the same names (Fournier et al. 2012; Kristensen et al. 2016; R Core Team 2016). When modeling count (hereafter referred to as abundance) or biomass data, we included an offset sample area term in our models, which we calculated for each site by multiplying the area of benthic substrate sampled by the area of the Caton tray subsampled. We modeled count and biomass data with an offset term, rather than using count data standardized by meter squared, in order to account for sampling uncertainties within (as opposed to outside) the models (Gelman and Hill 2007). We compared Akaike information criterion (AIC) scores among a null model (i.e., no explanatory variables) and models with tailwater identity or an environmental factor (i.e., distance from dam, hydropeaking intensity, or dam height) as a fixed effect. We chose the model family based on the distribution of the data; ultimately the models used were either negative binomial or gamma for discrete and continuous data, respectively.

3.4 Results

3.4.1 Patterns of dominance and community structure

Within each tailwater, 3–7 families dominated the communities, accounting for 95% of total abundance. The ten most abundant families accounted for ~99% of total abundance (Table 3.1). Of the ten most abundant taxa within each tailwater, eight taxa occurred in at least four tailwaters: Acari (Class: Arachnida), Baetidae (Order: Ephemeroptera), Chironomidae (Order: Diptera), Hyalellidae (Order: Amphipoda), Hydropsychidae (Order: Trichoptera), Hydroptilidae (Order: Trichoptera), Platyhelminthes (Kingdom: Animalia), and Simuliidae (Order: Diptera; Table B.2 in Appendix B). Across all sites, we found that dominance values ranged from 0.19 to 0.95 (average 0.55), invertebrate genus richness ranged from 3 to 26 (average 10 genera), abundance ranged from 415 to >170,000 individuals*m^{-2} (average 42,125 individuals*m^{-2}), and biomass ranged from 0.3 to 125 g*m^{-2} (average 12.9 g*m^{-2}).

Tailwater invertebrate communities in the Colorado River Basin showed distinct community structure at the order and family levels with abundance and biomass data. Here, we chose to only present abundance data at the order level, since the patterns observed across biotic data and taxonomic level were consistent (Figure 3.2). There was clear separation in community space between tailwater communities ($F = 26.07$, $p = 0.001$), as well as between insect and non-insect orders along NMDS axis 1. Furthermore, hydropeaking intensity was associated with NMDS axis 1 ($r^2 = 0.62$) and dam height with NMDS axis 2 ($r^2 = 0.59$). Insect orders with complex life cycles (Ephemeroptera, Plecoptera, Trichoptera, Coleoptera, Diptera) were associated with the three tailwaters experiencing lower hydropeaking intensity, while non-insect orders (i.e., Lumbriculida, Gastropoda, and Veneroida) were generally associated with the four tailwaters experiencing higher hydropeaking intensity.

3.4.2 Effects of hydropeaking intensity

Hydropeaking intensity impacted insect and EPT taxa more severely than the full aquatic invertebrate community. Based on univariate generalized linear mixed models (GLMMs) for the full community dataset (i.e., all invertebrates, including non-insects), the model with hydropeaking as the main explanatory variable did not reveal an effect of dominance or genus richness, although it did perform better than a null model with no environmental predictors for both abundance and biomass (Table B.3 in Appendix B). However, models examining the insect and EPT data subsets showed that hydropeaking intensity clearly impacted richness, abundance, and biomass by improving model fit compared to the null model (Table B.4 and B.5 in Appendix B).

Biotic response variables for insects and EPT were generally lower in tailwaters experiencing high hydropeaking (Glen Canyon, Davis, Parker, and Hoover; see Table 3.1 for hydropeaking intensity values). For example, the percent biomass contributed by insects relative to non-insect invertebrates was several times higher downstream of the two dams that experienced the lowest levels of hydropeaking (Fontenelle and Navajo; Table 3.1). For EPT taxa, an inflection point is apparent for the proportion of biomass they comprised near a hydropeaking intensity of 0.15, indicating that even small amounts of hydropeaking diminished EPT biomass (Figure 3.3). For most models, tailwater identity and dam height improved models. These variables act as bulk proxies for a multitude of environmental variables such as temperature, nutrient loads, reservoir size, and latitude/longitude.

3.4.3 Proximity to dams negatively affects communities

To determine if dam effects diminish downstream, we examined models that included distance from dam as a fixed effect. Whereas the impact of hydropeaking intensity varied depending on the dataset examined (i.e., full community, insect, or EPT), distance from dam predominantly impacted richness regardless of data partitioning. For the full community dataset, including distance from dam in the model improved model fit for genus richness and dominance, but not for abundance and only slightly for biomass (Table B.3 in Appendix B). For the insect and EPT-only datasets, incorporating distance from dam improved fit for genus richness, but not for abundance or biomass (Table B.4 and B.5 in Appendix B). Genus richness largely increased with distance from dam for all three data partitions, including the full community (Figure 3.4). Within most tailwaters, increased distance from the dam was associated with increased diversity of insect and EPT taxa. The exceptions were Glen Canyon, where diversity was low and static throughout the tailwater, and Hoover, where diversity was low and decreased with distance.

3.5 Discussion

Our study showed that tailwaters downstream of large dams in the Colorado River Basin are dominated by 3-7 invertebrate taxa that comprised 95% of individuals. Many of these dominant taxa were non-insect, non-flying species and thus were unavailable to terrestrial consumers. Consistent with previous studies, aquatic insects and sensitive EPT taxa were negatively associated with hydropeaking intensity, which puts limits on the type and perhaps quality of the invertebrate food base. While total invertebrate abundance and biomass did not change throughout tailwaters, insect and EPT richness, abundance, and biomass all increased, suggesting that impacts of damming are most acute immediately downstream of dams.

3.5.1 Tailwaters favor the dominance of a few taxa

Hydropeaking dams generate highly modified and disturbed environments, which affects the suite of organisms that can inhabit downstream tailwaters (Céréghino et al. 2002; Kennedy et al. 2016; Kjærstad et al. 2018). Two studies examining terrestrial plant communities help to highlight the characteristics of organisms that become dominant as a result of anthropogenic disturbances. Tilman and Lehman (2001) described how weedy plant species become dominant as a result of human-induced changes, such as increases in atmospheric N deposition. Seabloom et al. (2003) suggested that invasive plant species dominance may be due to anthropogenic disturbance and the low dispersal abilities and rarity of native species. While our aquatic study system and organisms differ from these terrestrial examples, we observed congruent patterns.

Our study showed that in the highly modified tailwaters in the Colorado Basin a few invertebrate taxa dominated communities (largely Chironomidae, Baetidae, and Dreissenidae). These insect families include many generalist species that are likely to occur across a variety of flow conditions, a parallel with weedy terrestrial plant species. The quagga mussel (Dreissenidae: *Dreissena bugensis*) is a dominant invasive species that appeared within three tailwaters and is also capable of persisting in a variety of flow conditions including periodic desiccation (Ricciardi et al. 1995). The dominance patterns we observed were the result of species loss closer to the dam, rather than reductions in abundance, further suggesting that the presence of extreme ecological conditions, and not reduced productivity, was the mechanism favoring a few weedy species. This taxonomic dominance by only a few species was evident across the basin; seven of the ten most abundant taxa occurred at over half of the tailwaters.

Many of the most abundant taxa in Colorado River Basin tailwaters were non-insects that do not have a terrestrial phase during their life cycle. This may have important consequences for ecosystem function, particularly for energy flow into the terrestrial environment. Insects are the primary food base for many organisms in rivers, contributing energy to riparian and terrestrial consumers (Baxter et al. 2005).

Ultimately, the prevalence of invertebrate dominance locally and across the basin has negative implications for aquatic biodiversity within tailwaters, a type of habitat now widespread globally, even while total productivity may have remained unchanged.

3.5.2 Hydropeaking intensity negatively impacts aquatic insects

As predicted, hydropeaking intensity had a negative effect on insect and EPT richness, abundance, and biomass, although this effect diminished with increasing distance from dams. This suggests that hydropeaking could play a role in excluding EPT and other insect taxa immediately below dams in particular. Similarly, insect biomass was lowest in tailwaters experiencing high amounts of hydropeaking, suggesting that a lower amount of biomass will be available to riparian consumers at these tailwaters. We did not observe a negative relationship between hydropeaking intensity and biomass when all invertebrates were considered together, suggesting that hydropeaking puts limits on the type and perhaps quality of the invertebrate food base rather than the total available secondary production. In fact, the highest average biomass occurred downstream of a high hydropeaking intensity dam (Parker Dam; approx. 40 g per m^2) due to the hyper-abundance of large, invasive freshwater quagga mussels. Although we reported biomass as standing stock, rather than secondary production, the high invertebrate assemblage biomass values we observed suggest that these tailwater systems are highly productive (Fisher et al. 1982; Huryn and Wallace 2000; Tonkin et al. 2009; Tonkin and Death 2013).

3.5.3 Richness increases within 24 km downstream of dams

We show that richness and dominance, but not abundance or biomass, changed substantially within the 24 km downstream of the dams. Specifically, richness increased and dominance decreased further from the dam. Tailwater communities nearest the dams were largely dominated by non-insect taxa (e.g., Dreissenidae) or generalist insect taxa (e.g., Chironomidae). As distance from the dam increased and the dominance of certain taxa decreased, more taxa joined the community, yet whole community abundance and biomass remained relatively constant. While these general trends in richness and abundance are consistent with previous research (Bock et al. 2007; Gutierrez-Canovas et al. 2013; Ellis and Jones 2014), there are some subtle differences.

We continued to see increases in richness throughout the 24 km sampled in many tailwaters, whereas Ellis and Jones (2014) observed recovery plateau within 5 km. Similar to our findings, Ellis and Jones (2014) observed shifts in the relative abundance of certain invertebrate taxa, with filter feeders dominating communities directly downstream of dams. We found that the increase in insect and EPT diversity farther away from dams was driving the increase in community diversity and decreasing dominance. This suggests that more suitable conditions exist for these taxa farther from the dam, more so than for non-insect taxa.

The two exceptions to this trend were the tailwaters downstream of Glen Canyon and Hoover Dams, which showed a constant or a slight decrease in richness throughout the 24 km stretch, respectively. Within the sampled reach, the Hoover tailwater starts to merge with the reservoir behind Davis Dam, which we would expect to result in fewer macroinvertebrate taxa as this large river system shifts from a lotic to a deep-water lentic environment. The Glen Canyon tailwater is a highly studied system for which shifts in richness and abundance have been observed on the scale of 100s of kilometers (Kennedy et al. 2016). Knowing that these trends exist within the Glen Canyon tailwater at a larger (but not smaller) scale, it becomes even more interesting that we observed species recovery within other tailwaters at this small scale. Within these other tailwaters (i.e., Fontenelle, Navajo, Flaming Gorge, Davis, and Parker) conditions shifted to favor terrestrially-available aquatic insects and sensitive EPT taxa that are more available to terrestrial consumers, ultimately increasing energy transfer from aquatic to riparian ecosystems and increasing biodiversity in these highly modified ecosystems.

3.5.4 Conclusion

Our study provides a spatially extensive dataset of the aquatic invertebrate communities in the Colorado River Basin. Patterns that we describe pertaining to how hydropeaking may be structuring the insect and non-insect components of aquatic communities informs river management with respect to invertebrate biodiversity conservation. Downstream of Glen Canyon Dam, for instance, experimental flow releases are being implemented specifically for the benefit of aquatic insects (Duke 2018). However, in addition to experimental flows, we can utilize long-term datasets from tailwaters to elucidate how specific shifts in environmental conditions, such as changes in hydropeaking levels from year to year, affect insect populations and communities temporally (Ruhi et al. 2018). These data can then help parameterize predictive models for dam practitioners to tailor their management actions for particular targets (Shenton et al. 2012; Yen et al. 2013; Tonkin et al. 2018; Rogosch et al. 2019). While focusing management actions on specific taxa (e.g., EPT taxa and insects) may have drawbacks for other members of the aquatic community, identifying how dam management practices impact specific biotic components informs holistic ecosystem management.

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Table 3.1 Patterns of dominance within tailwaters throughout the Colorado River Basin.

Tailwater	Hydropeaking Index	Average dominance (SE)	# taxa to reach 95% abundance	% abundance contributed by 10 most abundant taxa	# insect taxa of 10 most abundant taxa	% biomass contributed by insects	Average total biomass ($g*m^{-2}$) (SE)
Fontenelle	0.01	0.32 (0.06)	5	99.0%	9	96.3%	5.0 (1.62)
Navajo	0.02	0.60 (0.08)	4	99.5%	5	95.2%	3.7 (0.91)
Flaming Gorge	0.13	0.51 (0.01)	3	99.8%	8	19.3%	18.4 (2.67)
Glen Canyon	0.17	0.64 (0.06)	3	100%	3	50.1%	15.8 (3.7)
Davis	0.36	0.58 (0.1)	3	99.6%	5	2.2%	4.0 (1.45)
Parker	0.4	0.48 (0.09)	7	99.0%	5	0.6%	39.8 (19.05)
Hoover	0.56	0.36 (0.03)	4	100%	3	26.9%	3.2 (1.85)

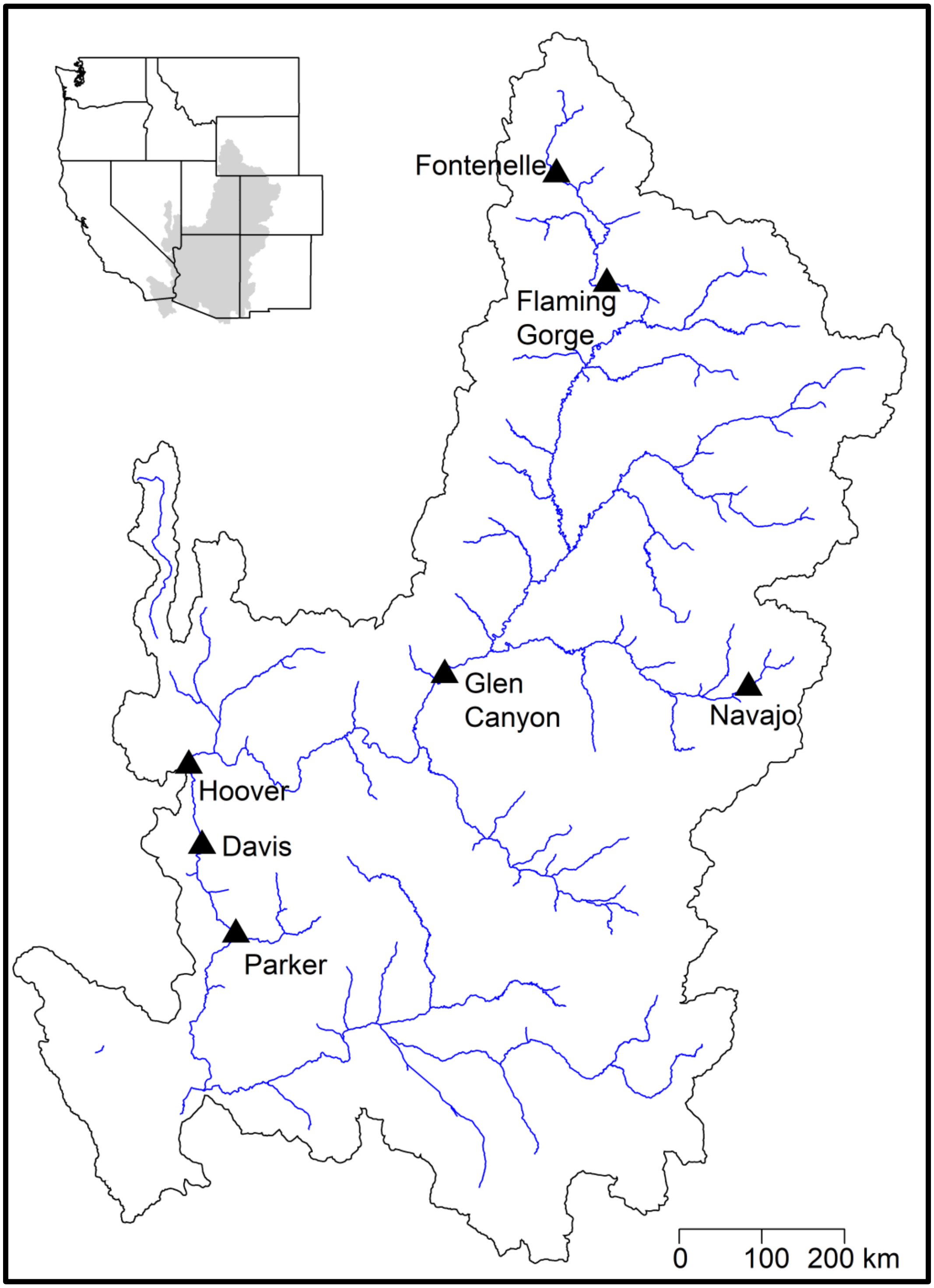

Figure 3.1 Map of the Colorado River Basin showing major tributaries and the dams upstream of the tailwaters sampled for this study.

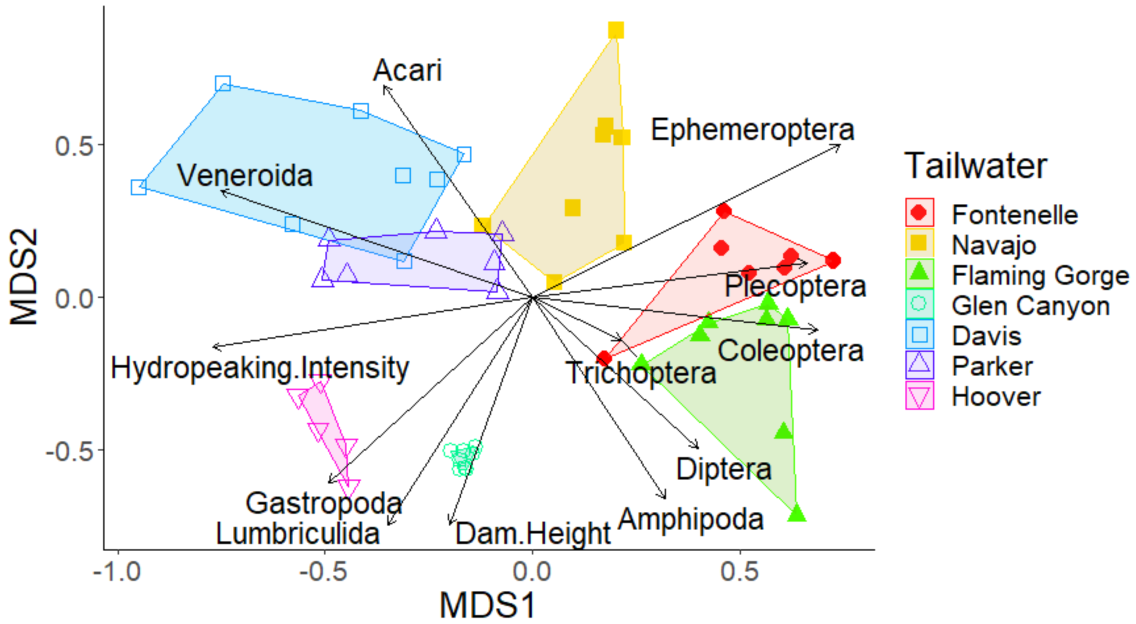

Figure 3.2 Non-metric multidimensional scaling plot (stress value 0.18) showing the log-adjusted abundance at the order level (or the lowest taxonomic level above order) with vectors showing the 10 most abundant taxa.

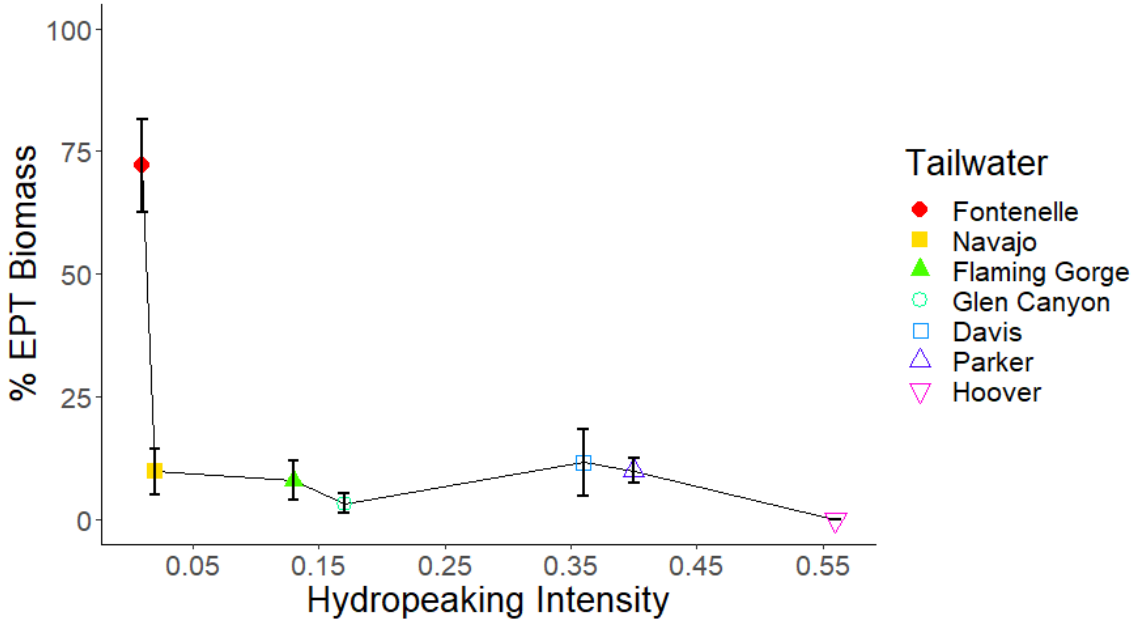

Figure 3.3 Proportion of EPT biomass shown as an average across all sites collected downstream of each dam graphed against hydropeaking intensity. Bars represent standard error.

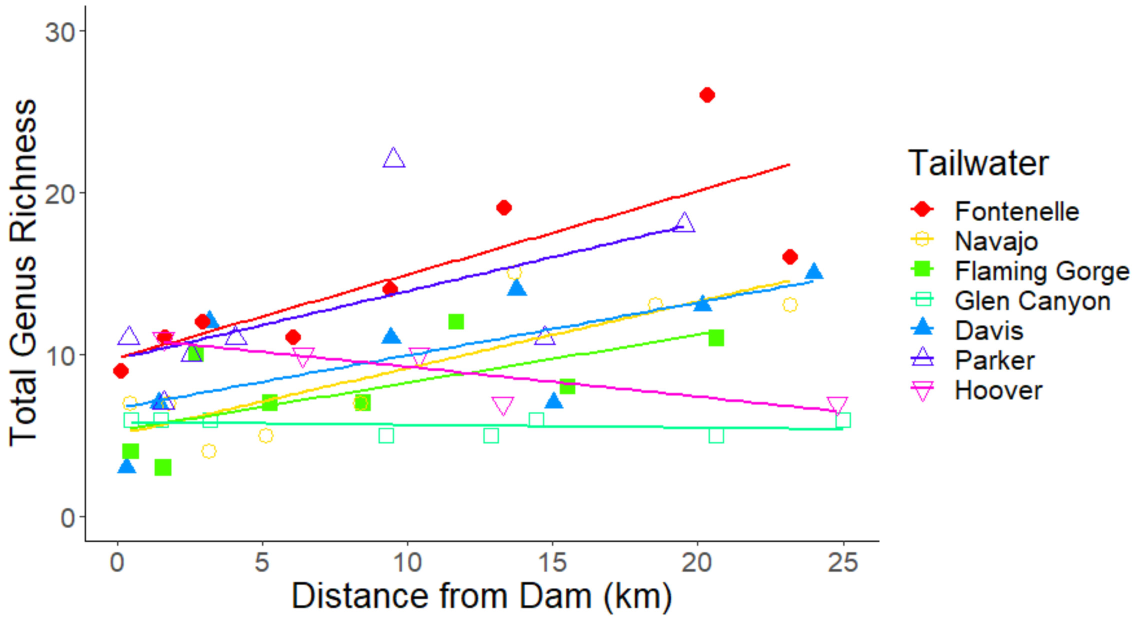

Figure 3.4 Genus (or the lowest feasible taxonomic level) richness as a function of distance from dam for all taxa observed at each site. Colors represent different tailwaters.

Chapter 4 – Population connectivity of aquatic insects in a dam-regulated, desert river

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4.1 Abstract

Landscapes are naturally fragmented, and humans have exaggerated this fragmentation, negatively impacting species dispersal and reducing population connectivity. Landscape fragmentation is especially severe in river ecosystems, where aquatic insects are generally limited to two primary modes of dispersal: downstream drift in the aquatic juvenile life stages and flight during the terrestrial winged adult stage. The stretches of river downstream of large hydropower dams can be uninhabitable for incoming (drifting) juvenile insects, while tributaries provide suitable habitat. The ability of adult aquatic insects to traverse river systems in search of suitable tributary habitat likely depends on factors such as species-specific dispersal ability and distance between tributaries. To explore the intersection of natural and human induced landscape fragmentation on aquatic insect dispersal ability, we quantified population genetics of three taxa with varying dispersal abilities, a caddisfly (Hydropsychidae: *Hydropsyche oslari*), a mayfly (Baetidae: *Fallceon quilleri*), and a water strider (Veliidae: *Rhagovelia distincta*), throughout tributaries of the Colorado River in the Grand Canyon, Arizona, USA. Using 2bRAD reduced genome sequencing and landscape genetics analyses, we revealed a strong pattern of isolation by distance among mayfly populations, while caddisfly and water strider populations were largely panmictic. Analysis of thousands of informative single nucleotide polymorphisms showed that realized dispersal ability may not be accurately predicted by species traits for these widespread species. Principal components analysis revealed a strong

division between caddisfly populations on the North Rim vs. South Rim, suggesting that the Colorado River itself imposes a dispersal barrier for this species. Our use of genetic tools in the Grand Canyon to understand population structure has enabled us to elucidate dispersal barriers for aquatic insects. Ultimately, these data can be used to inform effective conservation management plans for understudied organisms of conservation interest.

4.2 Introduction

Fragmentation occurs naturally as a result of the Earth's landscape, and anthropogenic alterations have exacerbated fragmentation by creating novel barriers that impede dispersal (Haddad et al. 2015). Natural fragmentation can by caused by certain ecosystems and geography, e.g., deserts and mountains respectively (Bleich et al. 1990; Bradford et al. 2003). Additionally, anthropogenic fragmentation can be caused by timber harvesting practices, e.g., clearcutting, that create forest patches and the damming of rivers (Khazan 2014; Grill et al. 2019). These anthropogenic barriers can be obvious, e.g., a dam that prevents the upstream movement of fish, or more nuanced, e.g., a dam that delays fish migration by altering water temperatures (Lundqvist et al. 2008; Marschall et al. 2011). In a world that is heavily impacted by humans, understanding how organisms disperse through fragmented landscapes is critical for preventing extinctions.

Dispersal is a fundamental component of ecology and evolution that helps protect against extinction, especially those species made up of small, isolated populations. Dispersal via metapopulation dynamics helps to counteract demographic, stochastic, and genetic processes that could lead to extinction (Hansson et al. 1992). Yet fragmentation, as well as the morphological and life history characteristics of species, mediates the ability of populations to disperse (Phillipsen et al. 2015; Poff 1997). Dispersal patterns have evolved over millennia to overcome harsh environmental barriers separating breeding populations (Saastamoinen et al. 2017). In this paper, we examine how both natural and anthropogenic barriers affect the dispersal of aquatic insects in a desert ecosystem.

Aquatic insects are a functionally critical component of river ecosystems; from serving as the food source for many aquatic and riparian species to increasing water quality by filtering particles from river water (Suter & Cormier 2015). As such, aquatic insects are the focus of growing conservation attention and their patterns of dispersal, while largely unknown, are of increasing interest (Duke 2018; Tonkin et al. 2018). Many aquatic insects have a complex life cycle with an aquatic juvenile followed by an aerial adult life cycle, which enables dispersal to happen along several avenues (Downes & Reich 2008). Juveniles can actively crawl or swim upstream or passively float downstream, and adults can actively fly to new habitats or passively disperse on wind currents. The success of a species to utilize particular dispersal methods (i.e., strength of dispersal) is dependent on both the physical characteristics of a species, i.e., body size and wing length, as well as the surrounding environmental conditions (Poff 1997). Traits can be used to make predictions about a species' dispersal strength (i.e., low, moderate, or high), and genetic tools can be used to test these predictions in different environments.

Additionally, genetics techniques and theory can be utilized to understand the underlying evolutionary mechanisms of dispersal and fragmentation. If dispersal strength is low, populations could become fragmented and experience genetic drift (i.e., genetic change due to chance). When dispersal strength is high, it is likely that populations would experience gene flow (i.e., transfer of genetic material from one population to another). If dispersal is high enough, this could lead to panmixia, in which all individuals in a population are potential mates. If dispersal strength isn't quite that high (i.e., it's of moderate strength), the evolutionary mechanism with the most influence could be isolation by distance, in which pairs of populations close to each other will be more genetically similar to each other than populations farther away from each other. The relationship between genetic distance and geographic distance can provide insight into dispersal strength and possible evolutionary mechanisms. When species exhibit high genetic distance (i.e., F_{ST} values) and high variance regardless of geographic distance between sampling points, this indicates low dispersal ability and possible population fragmentation (Figure 4.1 Panel A). When species exhibit low genetic distance and low variance regardless of geographic distance, this indicates high dispersal ability and high amounts of gene flow, a pattern consistent with panmictic population structure (Figure 4.1 Panel B). A species that exhibits a positive relationship between genetic and geographic distance indicates moderate dispersal abilities and possible isolation by distance (Figure 4.1 Panel C). While many aquatic insects in desert ecosystems have evolved to effectively disperse in these harsh environments, others experience population fragmentation (Cañedo-Argüelles et al. 2015). Over geologic time scales, fragmentation can allow populations to evolve locally, via genetic drift, as well as through adaptive evolution (Lytle et al. 2008; Phillipsen et al. 2015). Over shorter time scales, humans have fragmented landscapes causing small and isolated populations that are more vulnerable to extinction. Understanding these dynamics is critical to predicting how species exist in and move through fragmented landscapes.

The Colorado River is a large, desert river that flows for >400 km from Glen Canyon Dam, through the Grand Canyon, and to the inflow of Lake Mead. River flows of the mainstem in the canyon are heavily regulated by Glen Canyon Dam, which is located just upstream from the Grand Canyon. The aquatic invertebrate diversity of the Colorado River is low, with 12 invertebrate genera of mostly non-insects (Kennedy et al. 2016), while the tributaries that connect with the Colorado River harbor more diversity, with over 42 insect genera (Oberlin et al. 1999). The mainstem of the Grand Canyon is highly modified by hydropeaking (i.e., daily flow fluctuations associated with hydropower generation) from Glen Canyon Dam, which render the mainstem uninhabitable for most insect species (Kennedy et al. 2016). While no extensive, pre-dam historic data for aquatic invertebrates in Grand Canyon exist, current invertebrate communities upstream of the Glen Canyon Dam impoundment in Cataract Canyon are dominated by insect taxa (Haden et al. 2003). Given this and the presence of insects in the tributaries that could act as source populations, it is possible that many aquatic insect taxa were extirpated from the mainstem and that stressors currently exist that prevent recolonization. In addition to the modified flow regime of the mainstem acting as a barrier, the Grand Canyon also presents natural barriers to the dispersal of tributary insect populations, as it is a deep canyon (average of 1600 m) located in a harsh desert ecosystem (Stevens 2012). This ecosystem presents the opportunity to study how aquatic insects move through a landscape that presents both human and natural barriers to dispersal. We can test the influence of these barriers by examining whether river network distance (i.e., distance between points as traced along the mainstem of the Colorado) or Euclidian distance (i.e., straight line distance) is more predictive of genetic distance. If river network distance is more informative, it is likely that the mainstem is not a barrier and that the deep canyon walls act as a natural dispersal barrier. If Euclidian distance is more informative, that would suggest that insects are dispersing up and over the steep canyon walls, and that the mainstem of the Colorado River is a potential dispersal barrier.

We predicted (H1) the relationship between a species' genetic distance and geographic distance would be mediated by adult dispersal ability. Specifically, we predicted that species with low adult dispersal ability (in this study, a water strider), would be most influenced by genetic drift; species with high dispersal ability (a caddisfly) would be most influenced by gene flow; and species with moderate dispersal ability (a mayfly) would show isolation by distance (IBD). We predicted (H2) for species most heavily influenced by IBD that Euclidian distance would be a better predictor than river network distance, and that species most influenced by genetic drift and gene flow would show no influence of geographic distance on genetic differentiation. If Euclidian distance is a better predictor than river network distance for species experiencing IBD, that would indicate that the hydrologically altered mainstem of the Colorado River is a greater dispersal barrier than the naturally steep canyon geography.

4.3 Methods

4.3.1 Study species

We chose three taxa for their widespread distribution and varied dispersal ability: a water strider (Veliidae: *Rhagovelia distincta*), a caddisfly (Hydropsychidae: *Hydropsyche oslari*), and a mayfly (Baetidae: *Fallceon quilleri*). We found water striders and mayflies at 11 tributaries and caddisflies at nine tributaries. In 1976, *R. distincta* was found at five out of 13 sampled Colorado River tributaries by

Polhemus & Polhemus, whereas *Rhagovelia* sp. was only found at one tributary by Oberlin (1999). Additionally, trait databases indicate that species in the genus *Rhagovelia* have weak adult dispersal and flying abilities, but are strong crawlers and swimmers (Vieira et al. 2006). Specifically, *Rhagovelia* have evolved a propelling fan on the middle leg that allows them to access fast-flowing streams (Santos et al. 2017). There is little population genetic information on water striders, although evolution of sexually-selected traits appear to have contributed to a trade-off with adult flying ability in some species (Crumière et al. 2019). Given their patchy distribution and the possibility of weak adult dispersal ability, we hypothesized that *R. distincta* is a weak disperser and should show patterns of strong among-population divergence due to genetic drift.

Adult *H. oslari* had been collected throughout the Grand Canyon at locations of varying distances from tributaries, suggesting that this species has a high ability to disperse (Kennedy et al. 2016). Trait databases suggest that adults, rather than the larvae, of the genus *Hydropsyche* are able to disperse large distances, as both sexes have strong adult flying strength (Vieira et al. 2006). Mitochondrial DNA data suggest high gene flow within *H. oslari* populations in the Grand Canyon may be occurring, with some isolation as a result of river network topology (Metcalfe et al. 2020). For these reasons we hypothesized that *H. oslari* is a strong disperser and should show a pattern of population panmixia.

Fallceon quilleri was collected throughout Grand Canyon tributaries on an initial collecting trip for this project, but this species is rarely observed in the mainstem of the Colorado River (Kennedy et al. 2016). Trait databases suggest that species in the genus *Fallceon* have weak flight dispersal as adults, but strong larval dispersal, as they occur abundantly in drift samples and have strong swimming abilities (Vieira et al. 2006). Previous studies using mitochondrial DNA suggested that *F. quilleri* is a strong disperser, potentially able to travel at least 64 river km throughout a river network (Zickovich & Bohonak 2007). However, more recent research using restriction site-associated DNA methods showed population fragmentation at small spatial scales (1.4 km) along an elevation gradient in two mayfly species in a related genus *Baetis* (Polato et al. 2017). We hypothesized that *F. quilleri* is a disperser of moderate strength and should show a pattern of isolation by distance.

4.3.2 Study site and collection

During November 2016, we collected aquatic insects at the following Grand Canyon tributary creeks with perennially-flowing water: Clear, Hermit, Boucher, Crystal, Shinumo, Stone, Tapeats, Deer, Kanab, Havasu, National, Spring, Three Springs, and Diamond (Figure 4.2). These tributaries experience flows from less than 0.05 cubic meters per second (m^3/s) to around 3 m^3/s, outside of flood conditions. This is orders of magnitude less than the mainstem of the Colorado River, which experiences dam-regulated flows from 225-850 m^3/s. Samples were collected with handheld aquarium nets or D-nets with 500 micron mesh within 200 m of the confluence of the tributary with the mainstem of the Colorado River and stored in ethanol on ice until samples were transferred to a -20 freezer within two weeks. To estimate within tributary genetic variation, a second sample was taken approximately 1.5 km from the confluence. This within-tributary repeat sampling was done once for each species. In addition to Grand Canyon tributaries, we opportunistically collected *F. quilleri* at three sites elsewhere in the Colorado River Basin. We collected at two large rivers that flow into the Colorado, the San Juan River (near Bluff, Utah) and the Green River (near Green River, Utah) and a tributary of the Colorado River, Grandstaff Canyon (near Moab, Utah). At least 30 individuals were collected at each location, but final sample sizes used in the analyses were lower (approximately 12 individuals) due to variable extraction and sequencing success rates.

4.3.3 Multilocus SNP genotyping

To estimate genetic relatedness, we conducted multilocus SNP genotyping on all individuals. We extracted genomic DNA from each individual using the Zymo Quick DNA 96 Kit (Zymo Research Corporation, Irvine, CA). We used the 2bRAD (restriction site-associated DNA) protocol, a stream-lined and cost-effective method for genome-wide SNP genotyping. To create SNP libraries we used the reduced tag representation method described by Wang et al. (2012), which uses a selective adaptor to target approximately ¼ of the AlfI sites in the genome. This approach provided an appropriate balance in the trade-off between number of markers and sample sizes.

We combined libraries in equimolar amounts for sequencing in a single lane of 75-bp single-end reads on Illumina HiSeq 4000 at University of Oregon's Genomics and Cell Characterization Core Facility. We analyzed the resulting data using a *de novo* reference produced from 20 individuals sequenced from each species using the method of Snelling et al. (2017). Briefly, we filtered reads prior to analysis to exclude any low-quality or uninformative reads (Joint Genome Institute, 1997), and then aligned reads to the reference using SHRiMP (Rumble et al., 2009). We then called genotypes based on nucleotide frequencies at each position, calling loci homozygous if a second allele was present at less than 1%, heterozygous if present at >25%, and leaving the genotype undetermined at intermediate frequencies where genotypes could not be confidently determined from allele frequencies (Wang et al. 2012). Genotypes for each individual were called with a threshold of ≥5x coverage to include a larger number of loci. The scripts used for this analysis are available at https://github.com/Eli-Meyer/2brad_utilities.

4.3.4 Population genetics analysis

We reported the following population genetics statistics for each species at each sampling location, H_o (observed heterozygosity), H_s (observed diversities), and

F_{IS} (inbreeding coefficient). We used the *basic.stats* function in the R software "hierfstat" package to calculate these values (Goudet et al. 2020; R Core Team 2016). We then calculated pairwise F_{ST} values using the "RpairwiseFST.R" code developed by Giannico (2017). Data were graphed against pairwise geographical distances between all sampling locations along the river network to show the relationship between genetic and physical distance. To determine whether distances along the river network or Euclidian distances was more predictive of genetic distance, we ran generalized linear mixed models (GLMMs) using the *glm.nb* function in the R "MASS" package (Ripley et al. 2020). We chose the model family (i.e., negative binomial) based on the discrete nature of F_{ST} data (i.e., values 0-1). Euclidian distances were calculated using the *pointDistance* function in the R "raster" package (Hijmans et al. 2020). We completed a principal components analysis (PCAs) using the R "SNPRelate" package (Zheng et al. 2019). For the PCAs outliers were removed and the following PCAs were included with hulls and colors delineating sampling locations: each species with individuals collected within the Grand Canyon, each species with individuals collected at two locations within one tributary, and *F. quilleri* collected both within and outside of the Grand Canyon.

4.4 Results

4.4.1 Sequencing yield and SNP genotyping

To analyze genetic relationships among populations and associations with geographical distance, we sequenced 416 million high-quality reads, averaging 0.7-1.3 million reads per individual depending on the species (Table 4.1). We mapped these reads to a de novo reference for each species. After identifying a large number of putative polymorphisms for each species, we further filtered genotypes to minimize missing data and genotyping errors, identifying a set of high-quality SNPs that we used for all subsequent analyses (*R. distincta* had 8,963 SNPs, *H. oslari* 6,365 SNPs, and *F. quilleri* 1,851 SNPs).

4.4.2 Population genetics analysis

Population metrics revealed that all three species have similar observed heterozygosities (H_o), observed gene diversities (H_s), inbreeding coefficients (F_{IS}), and allelic richness (AR; Table 4.2). The average H_o for *R. distincta* was 0.62 (range: 0.59-0.67), *H. oslari* 0.59 (range: 0.55-0.63), and *F. quilleri* 0.54 (range: 0.52-0.58). The average H_s for *R. distincta* was 0.37 (range: 0.35-0.39), *H. oslari* 0.33 (range: 0.29-0.35), and *F. quilleri* 0.31 (range: 0.29-0.37). The average F_{IS} for *R. distincta* was -0.64 (range: -0.70 to -0.52), *H. oslari* -0.69 (range: -0.80 to -0.63), and *F. quilleri* -0.73 (range: -0.80 to -0.67). The negative F_{IS} values suggest highly heterozygous offspring as opposed to highly inbred ones (Johnson and Shaw 2015). The average AR for *R. distincta* 1.46 (range: 1.42-1.52), *H. oslari* 1.42 (range: 1.35-1.49), and *F. quilleri* 1.41 (range: 1.38-1.53).

To determine whether the hypothesized evolutionary patterns of genetic drift, gene flow, and isolation by distance were followed for species with differing dispersal abilities, we examined the relationships between genetic distance (F_{ST}) and geographic distance along the river network. Both *R. distincta* and *H. oslari* showed low F_{ST} values (less than 0.2) regardless of distance between sampling points, slopes of zero, and intercepts near zero (0.03 and 0.06 respectively) indicating high dispersal ability and high amounts of gene flow for both (Figures 4.3 and 4.4 respectively). *F. quilleri*, on the other hand, had relatively high F_{ST} values (0.1-0.5) and the degree of genetic distance was positively related to geographic distance (Figure 4.5). Samples were more genetically distinct the farther apart they were physically collected, indicating moderate dispersal abilities and isolation by distance. This trend was maintained for *F. quilleri* samples that were collected outside the Grand Canyon as well (Appendix C, Figure C.1).

We used GLMMs to determine whether geographic distance along a river network or straight-line Euclidian distance was a better predictor of genetic similarity (Table 4.3). For both *R. distincta* and *H. oslari*, the inclusion of either distance metric did not substantially improve model performance, suggesting that geographic distance does not influence population structure of these panmictic species, at least at the spatial scales examined in this study. For *F. quilleri* both Euclidian and river kilometer distances were more informative than the null model, although there was not much difference between the two distances (ΔAIC = 1.6).

PCA results complimented the results of the F_{ST} data by indicating potential population fragmentation. *R. distinca* showed only slightly more structure with one sampling location (Kanab Creek) appearing to be different (Figure 4.6). *H. oslari*, on the other hand, showed a pattern suggesting that the Colorado River itself forms a strong barrier to gene flow. Tributaries from the North Rim vs. South Rim generally separated along the x-axis, which represented Eigenvector 1 (Figure 4.6). The one exception is Spring Creek, which is located on the North Rim but is associated with the two other South Rim tributaries, Havasu and Three Springs. While there was much overlap between genotypes observed across sampling locations for *F. quilleri* within Grand Canyon tributaries (Figure 4.6), when sites from outside the Grand Canyon were included, there was clear separation of population within vs. outside the Grand Canyon (Appendix C, Figure C.2). Lastly, we sampled each species twice within one tributary to reveal within-tributary variation. The PCAs showed little evidence of differentiation between sampling locations separated by 1.5 km of contiguous tributary habitat (Appendix C, Figures C.3-C.5).

4.5 Discussion

We found that our hypotheses concerning dispersal ability based on traits and spatial distribution did not always align with the genetic evidence. Both *R. distincta* and *H. oslari* showed evidence for are relatively high dispersers, whereas *F. quilleri* is a moderate disperser. For *R. distincta*, this finding contradicts our prediction that this water strider would be a weak disperser, a prediction based on trait databases (i.e., describing the genus *Rhagovelia* have weak adult dispersal and flying abilities; Vieira et al. 2006). Additionally, we found evidence of a relatively distinct population of *R. distincta* at Kanab Creek, which could be a result of this tributaries unique geography. Kanab Creek is a North Rim tributary that flows for >200 km, thus insects in this tributary had access to more habitat and potentially more mates and genetic variation than insects in the other shorter tributaries that were sampled.

Furthermore, *H. oslari* generally showed population structure between tributaries on the North Rim vs. South Rim. Metcalfe et al. (2020) found a very similar separation between *H. oslari* populations in the Grand Canyon utilizing mitochondrial DNA. The authors attributed this to the influence of volcanic flows and natural damming near the Toroweap Fault on the historic dispersal and genetic mixing of *H. oslari*. The Toroweap Fault is located ~300 km downstream of Glen Canyon Dam and separates the eastern and western portions of the Grand Canyon. By sampling two more locations within Grand Canyon than Metcalfe et al. (2020), we believe that there is evidence to support a division by watershed orientation (North vs South Rim) in addition to the division at the Toroweap Fault. This could explain why Spring Creek, located on the North Rim and below the Toroweap Fault, grouped with the other two South Rim tributaries. All other North Rim tributaries are upstream of the Toroweap Fault.

Our study reveals that fragmentation does play a role within this desert landscape, but our study did not distinguish whether the observed population structure was a result of natural geography or anthropogenic alteration of the mainstem flows in the Colorado River. Evidence in support of one barrier having more influence over the other would have been seen in the GLMM results. We would have expected one model (Euclidian or river network distance) to perform better than the other. At least for *F. quilleri,* a species exhibiting isolation by distance, this would have provided evidence towards the path of dispersal, whether along the river itself (i.e., river network distance) or up and over the canyon walls (i.e., Euclidian distance). While both models performed better than the null for *F. quilleri*, there was very little difference between the AIC scores of either model. Regardless of the source of the barrier, there is fragmentation between some Grand Canyon tributary populations and eco-evolutionary dynamics can help to understand these species' movements.

Our study shows eco-evolutionary patterns for high and moderate dispersers that closely resemble those observed by Phillipsen et al. (2015) for three other desert insect species. *R. distincta* and *H. oslari* were both found to be high dispersers with gene flow appearing to be more influential than genetic drift. Populations of both species appear to be panmictic because there was no relationship between genetic distance and geographic distance, the intercept was small, and the variance was low across all geographic distances. *F. quilleri* was predicted to be a moderate disperser, most impacted by isolation by distance. We found evidence to support this with the positive relationship between genetic distance (F_{ST}) and geographic distance (river network). The intercept was near zero, and the variance increased with increasing geographic distance (Appendix C, Figure C.1). Genetic tools can effectively be used to understand the underlying evolutionary mechanisms that influence ecological dynamics, such as dispersal. This population genetic information allows us to better understand the barriers that exist to dispersal, which is especially useful for conservation when basic biological and life history information on species of concern is unavailable.

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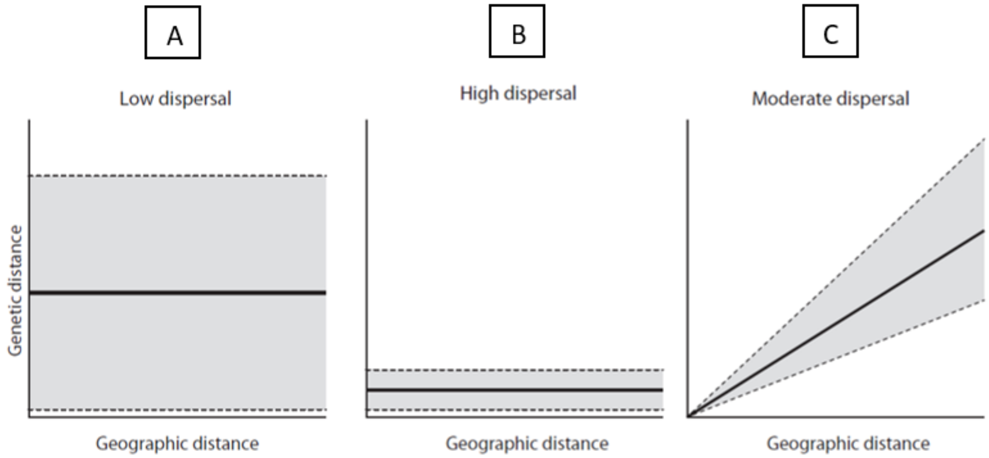

Figure 4.1 Predicted relationships between genetic and geographic (Euclidean) distances between pairs of populations. The black line is the regression line, and the shaded area shows the variance in the pairwise genetic distances across the geographic distances. When genetic drift is more influential than gene flow (A), as is predicted for species with low dispersal, the slope of the line should not differ significantly from zero, the intercept will be high, and the variance will be high across all geographic distances. Gene flow should be more influential than drift for species with high dispersal (B). The regression line in this case should not significantly deviate from zero, the intercept should be small, and variance is low across all geographic distances. For species with moderate dispersal, a positive slope is predicted (C). The intercept should be near zero, and variance should increase with increasing geographic distance. Modified from Phillipsen et al. 2015.

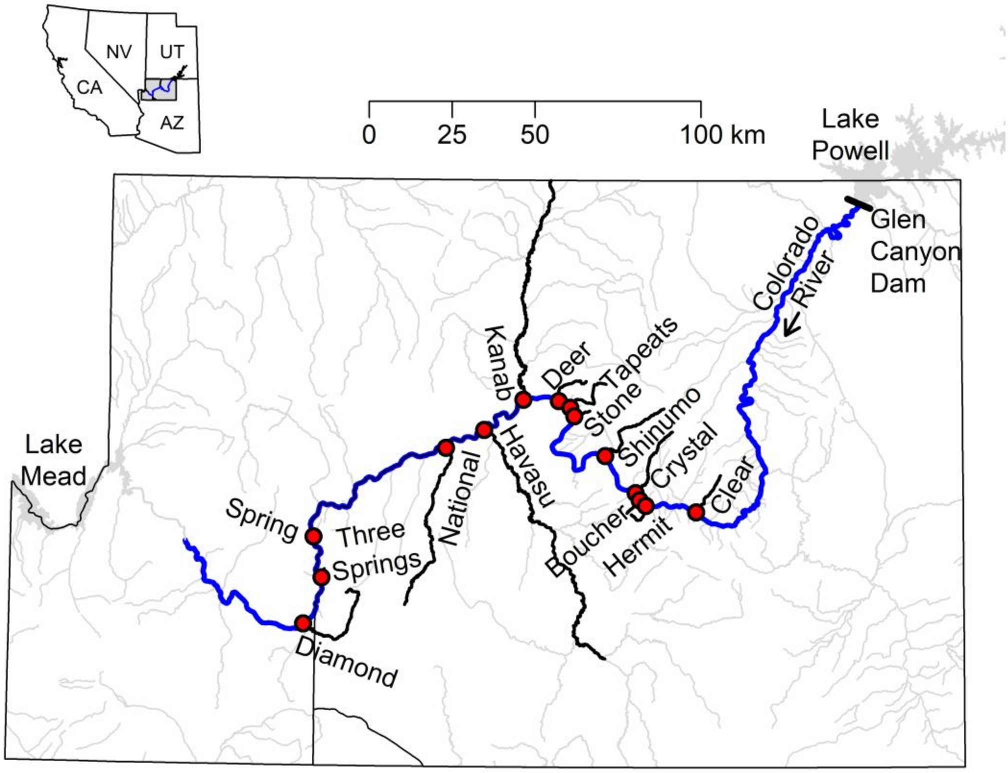

Figure 4.2 Map of the Colorado River through Grand Canyon (blue line) and tributaries. Tributaries where samples were collected are labeled by name and are highlighted with thicker black lines.

Table 4.1 Summary of sequencing yields and processing efficiencies for 2bRAD.

	R. distincta	*H. oslari*	*F. quilleri*
Number of individuals	156	105	160
Number of source tributaries	11	9	11
Raw sequencing depth (millions)	222	161	217
HQ sequencing depth (millions)	108	107	201
HQ reads per sample (millions)	0.7	1.0	1.3
Putative polymorphisms	15,936	12,764	10,918
High-quality SNPs	8,963	6,365	1,851

Table 4.2 Population sampling locations (Tributary), sample sizes (n), geographic coordinates (UTM E and UTM N) and population metrics for *Rhagovelia distincta*, *Hydropsyche oslari*, and *Fallceon quilleri* in the tributaries of the Grand Canyon, Arizona, and the San Juan River, Grandstaff Canyon, and Green River, Utah. The population metrics reported are observed heterozygosities (H_o), observed gene diversities (H_S), inbreeding coefficients (F_{IS}), and allelic richness (AR).

Species	**Tributary**	***n***	**Latitude**	**Longitude**	H_o	H_S	F_{IS}	**AR**
R. distincta	Upper Clear	12	36.094726	-112.031655	0.65	0.38	-0.70	1.48
	Hermit	12	36.099256	-112.20944	0.63	0.37	-0.66	1.47
	Lower Boucher	12	36.115482	-112.231126	0.62	0.37	-0.64	1.45
	Upper Boucher	13	36.106097	-112.239851	0.60	0.36	-0.65	1.42
	Crystal	12	36.135996	-112.242442	0.59	0.35	-0.67	1.43
	Shinumo	13	36.239026	-112.349599	0.60	0.36	-0.60	1.43
	Stone	14	36.346937	-112.453441	0.62	0.37	-0.64	1.45
	Deer	12	36.389285	-112.508255	0.62	0.37	-0.64	1.46
	Kanab	14	36.393327	-112.630376	0.60	0.37	-0.57	1.44
	Havasu	14	36.305515	-112.760989	0.67	0.39	-0.70	1.52
	Spring	14	36.018615	-113.352813	0.61	0.38	-0.52	1.43
	Three Springs	14	35.885733	-113.308031	0.63	0.38	-0.66	1.48
H. oslari	Crystal	3	36.135996	-112.242442	0.55	0.29	-0.80	1.49
	Shinumo	8	36.239026	-112.349599	0.61	0.32	-0.77	1.43
	Stone	15	36.346937	-112.453441	0.59	0.34	-0.63	1.40
	Lower Tapeats	11	36.371604	-112.468649	0.61	0.34	-0.69	1.43
	Upper Tapeats	11	36.385217	-112.459256	0.63	0.35	-0.67	1.48
	Deer	12	36.389285	-112.508255	0.61	0.34	-0.70	1.41
	Kanab	11	36.393327	-112.630376	0.55	0.31	-0.69	1.35
	Havasu	10	36.305515	-112.760989	0.58	0.33	-0.64	1.43

Table 4.2 *continued*

Species	**Tributary**	***n***	**Lat**	**Lon**	$\mathbf{H_o}$	$\mathbf{H_S}$	F_{IS}	**AR**
H. oslari	Spring	12	36.018615	-113.352813	0.59	0.33	-0.64	1.42
	Three Springs	12	35.885733	-113.308031	0.57	0.32	-0.67	1.38
F. quilleri	Lower Clear	12	36.082265	-112.035959	0.52	0.29	-0.75	1.39
	Hermit	11	36.099256	-112.20944	0.53	0.30	-0.76	1.39
	Lower Boucher	12	36.115482	-112.231126	0.52	0.29	-0.72	1.38
	Upper Boucher	12	36.106097	-112.239851	0.52	0.30	-0.76	1.40
	Crystal	15	36.135996	-112.242442	0.53	0.30	-0.74	1.38
	Shinumo	12	36.239026	-112.349599	0.53	0.30	-0.73	1.40
	Stone	12	36.346937	-112.453441	0.52	0.30	-0.73	1.38
	Kanab	14	36.393327	-112.630376	0.55	0.32	-0.75	1.40
	National	12	36.254781	-112.888185	0.53	0.29	-0.80	1.38
	Spring	12	36.018615	-113.352813	0.54	0.30	-0.77	1.39
	Three Springs	12	35.885733	-113.308031	0.56	0.32	-0.70	1.42
	Diamond	10	35.765413	-113.373136	0.54	0.32	-0.68	1.41
	San Juan River	6	37.258587	-109.618123	0.53	0.33	-0.76	1.47
	Grandstaff	3	38.609637	-109.533978	0.58	0.37	-0.67	1.53
	Green River	5	39.080142	-110.142451	0.56	0.32	-0.67	1.48

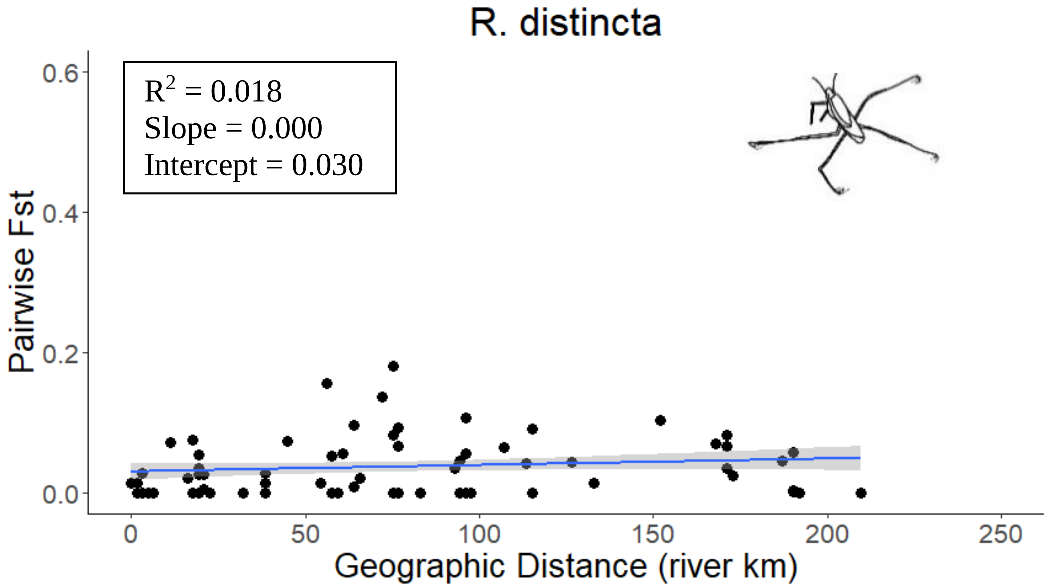

Figure 4.3 Empirical relationships between genetic distances (F_{ST}) and geographic distances (river km) between pairs of populations. The pattern found for *R. distincta* closely matched the predictions for high dispersal (see Fig. 4.1). Image credit for *Rhagovelia*: Isabelle Vincent.

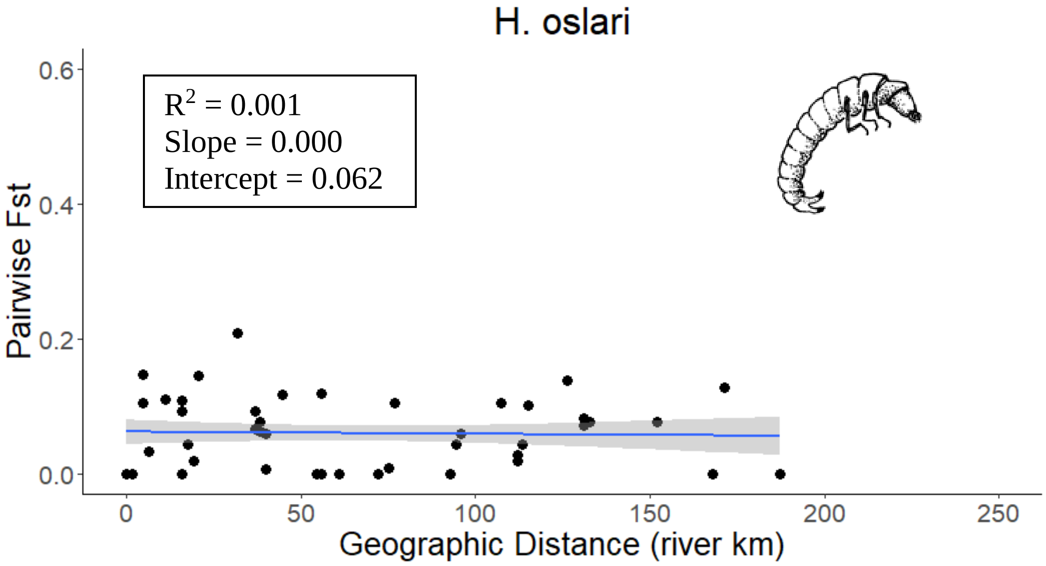

Figure 4.4 Empirical relationships between genetic distances (F_{ST}) and geographic distances (river km) between pairs of populations. The pattern found for *H. oslari* closely matched the predictions for high dispersal (see Fig. 4.1).

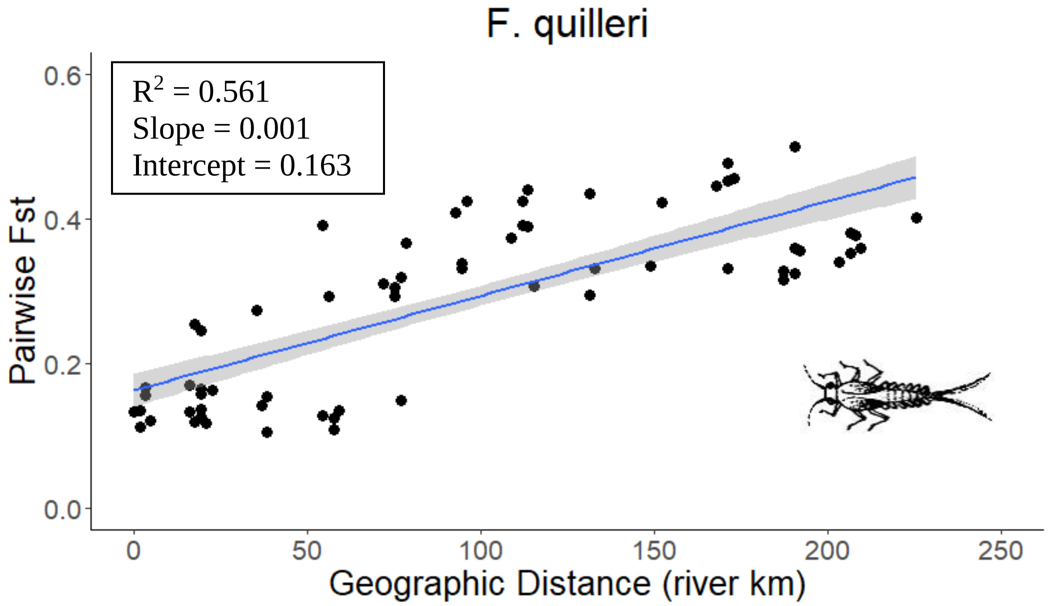

Figure 4.5 Empirical relationships between genetic distances (F_{ST}) and geographic distances (river km) between pairs of populations. The pattern found for *F. quilleri* closely matched the predictions for moderate dispersal abilities (see Fig. 4.1).

Table 4.3 Generalized linear mixed model AIC table for *Rhagovelia distincta*, *Hydropsyche oslari*, and *Fallceon quiller*. Models are ordered with increasing AIC scores.

Taxa	Response Variable	Model	AIC	ΔAIC
R. distincta	F_{ST}	Null	515.2	0.0
		Euclidian Distance	515.8	0.6
		River Distance	515.9	0.7
H. oslari	F_{ST}	Null	331.2	0.0
		Euclidian Distance	333.2	2.0
		River Distance	333.2	2.0
F. quilleri	F_{ST}	Euclidian Distance	956.9	0.0
		River Distance	958.5	1.6
		Null	1024	67.1

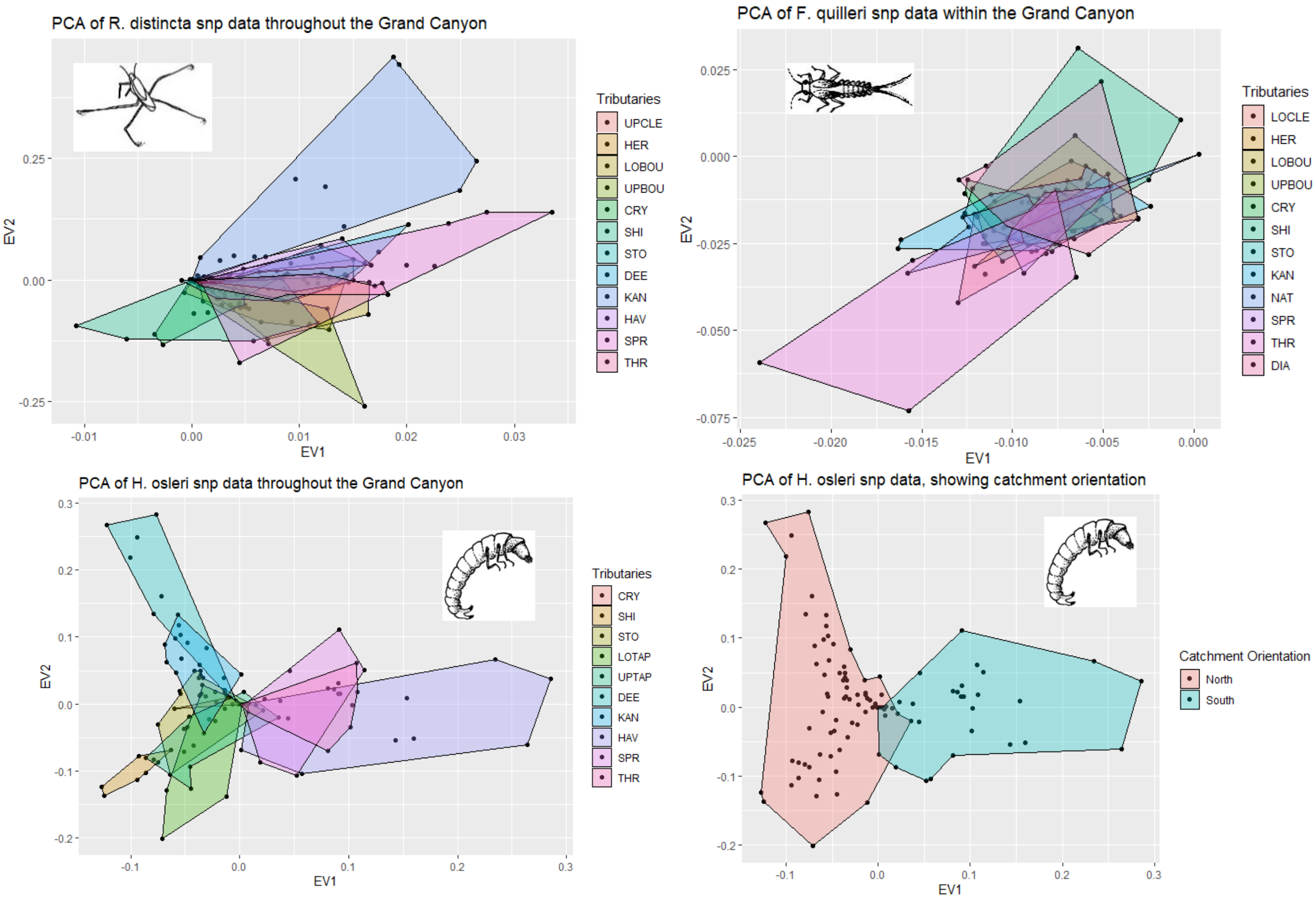

Figure 4.6 *R. distincta* population structure (top left), *F. quilleri* population structure (top right). *H. oslari* population structure showing each tributary and data divided by North Rim vs. South Rim (bottom right and left respectively). Image credit for *Rhagovelia*: Isabelle Vincent.

Chapter 5 – General Conclusions

Those who have privileges or are in leadership roles have a responsibility to work actively toward inclusivity, equity, and diversity while prioritizing the needs and voices of those who have been marginalized. Following challenges associated with the 2017 SFS meeting in Raleigh, North Carolina, and efforts made during the 2018 SFS meeting in Detroit, Michigan, to improve inclusion, I have helped compiled recommendations on how to create a more inclusive scientific society by listening to the needs of marginalized SFS members. However, the 2 examples of challenges and successes in addressing diversity within SFS described in this paper largely focus on only 2 identity dimensions (race and LGBTQ+ status). Moving forward, it is important for scientific societies and their members to recognize that work on inclusivity must be done across multiple visible and invisible identity dimensions (e.g., parental status, ability status, socioeconomic status, veteran status). From the individual to the scientific society level, I hope this paper serves to invite every SFS member to participate in actively increasing diversity, equity, and inclusivity within the field of freshwater science. In particular, I challenge individuals from the demographic majority or with privileged identities to commit to breaking down the barriers faced by marginalized scientists. I advocate that this work must continue for the advancement of science and scientists and that the collective effort of all SFS members is needed to make these actions possible.

In addition to looking at who is doing freshwater science, I wanted to examine how humans are altering freshwater ecosystems. My study of the Colorado River Basin tailwaters provides a spatially extensive dataset of the aquatic invertebrate communities in the basin. Patterns that I describe pertaining to how hydropeaking may be structuring the insect and non-insect components of aquatic communities informs river management with respect to invertebrate biodiversity conservation. Downstream of Glen Canyon Dam, for instance, experimental flow releases are being implemented specifically for the benefit of aquatic insects (Duke 2018). However, in addition to experimental flows, scientists can utilize long-term datasets from tailwaters to elucidate how specific shifts in environmental conditions, such as changes in hydropeaking levels from year to year, affect insect populations and communities temporally (Ruhi et al. 2018). These data can then help parameterize predictive models for dam practitioners to tailor their management actions for particular targets (Shenton et al. 2012; Yen et al. 2013; Tonkin et al. 2018; Rogosch et al. 2019). While focusing management actions on specific taxa (e.g., EPT taxa and insects) may have drawbacks for other members of the aquatic community, identifying how dam management practices impact specific biotic components informs holistic ecosystem management.

In addition to looking at community metrics to understand how dams impact freshwater ecosystems, it is imperative for conservation efforts that scientists also examine population genetics. My genetics study in the Grand

Canyon showed eco-evolutionary patterns for moderate and high dispersers that closely resemble those observed by Phillipsen et al. (2015) for three desert insect species. *F. quilleri* was predicted to be a moderate disperser, most impacted by isolation by distance. *R. distincta* and *H. oslari* were both found to be high dispersers with gene flow appearing to be more influential than genetic drift. Additionally, I found evidence of a historically isolated population of *R. distincta* at one tributary and that *H. oslari* showed population structure between tributaries on the North Rim vs. South Rim. This study revealed evolutionary patterns for aquatic insects with varying dispersal abilities and that fragmentation does play a role within this desert landscape. Genetic tools can effectively be used to understand the underlying evolutionary mechanisms that influence ecological dynamics, such as dispersal. This is especially useful when basic biological and life history information on species of conservation concern is unavailable.

I believe that most humans are fundamentally good people. It is the responsibility of those with education and privilege to use their knowledge and resources to disrupt systems of oppression that have been institutionalized for the economic gain of a few. These systems of oppression (i.e., systemic racism, sexism, heterosexism, ableism, classism, etc.) are harming people and through their interaction with economic and political systems (i.e., capitalism) are also harming our ecosystems. It is our moral responsibility to dismantle these systems by organizing with folx within our communities to create a society that is more just, equitable, sustainable, and loving. I believe that we can. We must.

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APPENDICES

Appendix A – Chapter 2 Suggested List of Resources

Books

- Adams, M., W. J. Blumenfeld, D. C. J. Catalano, K. Dejong, H. W. Hackman, L. E. Hopkins, B. Love, M. L. Peters, D. Shlasko, and X. Zuniga. (editors) *Readings for Diversity and Social Justice.* 2018. Routledge.
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- Opportunities for White People in the Fight for Racial Justice: Moving from Actor to Ally to Accomplice. Available at: https://www.whiteaccomplices.org/
- Diversify Ecology and Evolutionary Biology (EEB). Available at: https://diversifyeeb.com/
- Project Biodiversify: Tools for Promoting Diversity and Inclusivity in Biology Classrooms. Available at: https://projectbiodiversify.org
- Kim, M. (editor) Awaken Blog. Available at: https://medium.com/awaken-blog
- Dr. Chanda Prescod-Weinstein, Decolonising Science Reading List. Available at: https://medium.com/@chanda/decolonising-science-reading-list-339fb773d51f#.x0dvzakgw
- Priya Shukla, Diversity, Equity & Inclusion in Science: A Reading List. Available at: https://medium.com/@priyology/diversity-inclusion-in-science-a-reading-list-a45cea40b972
- Dr. Lauren Esposito et al., 500 Queer Scientists. Available at: https://www.500queerscientists.com
- Drs. Jane Zelikova and Kelly Ramirez, 500 Women Scientists. Available at: https://500womenscientists.org/
- Dr. Kat Milligan-Myhre, Resources for Women and Minorities in STEM. Available at: https://drkatlab.wordpress.com/resources/women-and-minorities-in-stem/

Reports

- Beasley, M. A. 2017. Beyond Diversity: A Roadmap to Building an Inclusive Organization. Green 2.0. Available at: https://www.diversegreen.org/beyond-diversity/?utm_campaign=briefly&utm_source=newsletter&utm_medium=email&utm_content=briefly&utm_term=EDIT%20Briefly
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Videos

- Kimberlé Crenshaw. “The Urgency of Intersectionality”. Available at: https://www.ted.com/talks/kimberle_crenshaw_the_urgency_of_intersectionality

- Fusion Comedy. "How Microaggressions are Like Mosquito Bites". Available at: https://www.youtube.com/watch?v=hDd3bzA7450

Podcasts and other Audio Media

- Barboza, M. The Femmes of STEM podcast. Available at: https://www.femmesofstem.com/
- NDN Science Show. Available at: https://ndnscienceshow.wordpress.com/
- NPR's Code Switch. Available at: https://www.npr.org/podcasts/510312/codeswitch

Institutional

- Institutional diversity & inclusion offices

Programs

- Scientific societies (e.g., Society for the Advancement of Chicanos and Native Americans in the Sciences, Macrolatinos, oSTEM)
- Institutional recruiting programs (e.g., EEB Diversity Preview Weekend at Cornell University, EEB at Princeton University)
- Funding mechanisms (e.g., National Science Foundation's Louis Stokes Alliances for Minority Participation, Ford Foundation Fellowships)
- The Hutton Junior Fisheries Biology Program. American Fisheries Society

Appendix B – Chapter 3 Supplementary Material

Table B.1 Characteristics of the large dams of the Colorado River Basin used in this study. All dams are managed by the U.S. Bureau of Reclamation. Flaming Gorge Dam was retrofit in 1977–1978 to install a selective withdrawal device to regulate water release temperatures.

Dam	River	Built	Design	Release type	Height (m)	Length (m)	Purpose	Installed capacity (MW)	Reservoir length (km)	Reservoir total capacity (megaliters)	Catchment area (km^2)
Fontenelle	Green	1961–1964	Earthfill	Hypolimnetic	42	1,652	1.Storage 2.Hydropower	10	32	425,995	10,764
Navajo	San Juan	1958–1963	Earthfill	Hypolimnetic	122	1,112	1.Storage 2.Hydropower 3.Flood control	32	56	2,107,524	8,262
Flaming Gorge	Green	1958–1964	Concrete thin-arch	Hypolimnetic	153	392	1.Storage 2.Hydropower 3.Flood control	152	146	4,673,286	38,850
Glen Canyon	Colorado	1956–1966	Concrete arch gravity	Hypolimnetic	216	475	1.Storage 2.Hydropower	1,320	299	33,303,960	280,586
Davis	Colorado	1942–1953	Earthfill	Hypolimnetic	60	490	1.Storage 2.Hydropower	251	108	2,242,837	448,845
Parker	Colorado	1934–1938	Concrete arch gravity	Epilimnetic	97	261	1.Storage 2.Hydropower	120	72	797,075	462,033
Hoover	Colorado	1931–1936	Concrete arch gravity	Hypolimnetic	221	379	1.Hydropower 2.Flood control 3.Storage	2,080	180	35,199,819	434,600

Table B.2 The ten most abundant families (or higher classification if not identified to family) within each tailwater, listed in order of decreasing abundance with non-insect taxa highlighted.

Fontenelle	**Navajo**	**Flaming Gorge**	**Glen Canyon**	**Davis**	**Parker**	**Hoover**
Baetidae	Chironomidae	Chironomidae	Chironomidae	Dreissenidae	Dreissenidae	Chironomidae
Hydropsychidae	Simuliidae	Hyalellidae	Lumbriculidae	Acari	Chironomidae	Hydrobiidae
Chironomidae	Acari	Baetidae	Hydrobiidae	Chironomidae	Hydropsychidae	Lumbriculidae
Ephemerellidae	Baetidae	Simuliidae	Trichoptera	Baetidae	Hydroptilidae	Gammaridae
Leptohyphidae	Platyhelminthes	Elmidae	Gammaridae	Hydroptilidae	Hyalellidae	Planariidae
Perlodidae	Crangonyctidae	Hydropsychidae	Platyhelminthes	Platyhelminthes	Corbiculidae	Dreissenidae
Elmidae	Ephemerellidae	Perlodidae	Simuliidae	Hydropsychidae	Simuliidae	Acari
Hyalellidae	Physidae	Platyhelminthes		Lymnaeidae	Acari	Annelida
Hydroptilidae	Glossosomatidae	Ephemerellidae		Physidae	Baetidae	Hemiptera
Heptageniidae	Hyalellidae	Hydroptilidae		Ceratopogonidae	Physidae	Trichoptera

Table B.3 Generalized linear mixed model AIC table for the full invertebrate community. Models are ordered with increasing AIC scores.

Taxa	Response Variable	Model	AIC	ΔAIC
All	Dominance	Tailwater	-22.2	0
		Distance	-18.6	3.6
		Null	-14.8	7.4
		Dam Height	-14.4	7.8
		Hydropeaking Intensity	-12.9	9.3
	Genus richness	Dam Height	288.0	0
		Tailwater	288.1	0.1
		Distance	296.0	8.0
		Null	303.3	15.3
		Hydropeaking Intensity	305.3	17.3
	Abundance	Tailwater	877.8	0
		Dam Height	891.6	13.8
		Hydropeaking Intensity	916.7	38.9
		Null	917.7	39.9
		Distance	919.5	41.7
	Biomass	Tailwater	771.9	0
		Hydropeaking Intensity	800.4	28.5
		Distance	802.9	31.0
		Null	804.5	32.6
		Dam Height	806.2	34.3

Table B.4 Generalized linear mixed model AIC table for data partitioned to insects only. Models are ordered with increasing AIC scores.

Taxa	Response Variable	Model	AIC	ΔAIC
Insect	Genus richness	Tailwater	258.6	0
		Dam Height	261.8	3.2
		Distance	281.3	22.7
		Hydropeaking Intensity	283.4	24.8
		Null	286.8	28.2
	Abundance	Tailwater	799.5	0
		Dam Height	843.1	43.6
		Hydropeaking Intensity	859.5	60.0
		Null	865.4	65.9
		Distance	866.5	67.0
	Biomass	Tailwater	589.6	0
		Hydropeaking Intensity	623.6	34.0
		Dam Height	634.1	44.5
		Null	635.2	45.6
		Distance	637.1	47.5

Table B.5 Generalized linear mixed model AIC table for data partitioned to EPT only. Models are ordered with increasing AIC scores.

Taxa	Response Variable	Model	AIC	ΔAIC
EPT	Genus richness	Tailwater	223.5	0
		Dam Height	225.7	2.2
		Hydropeaking Intensity	246.0	22.5
		Distance	246.6	23.1
		Null	253.3	29.8
	Abundance	Tailwater	556.8	0
		Hydropeaking Intensity	565.4	8.6
		Distance	583.0	26.2
		Null	585.1	28.3
		Dam Height	586.8	30.0
	Biomass	Tailwater	343.3	0
		Hydropeaking Intensity	378.3	35.0
		Dam Height	390.9	47.6
		Null	404.3	61.0
		Distance	406.1	62.8

Appendix C – Chapter 4 Supplementary Material

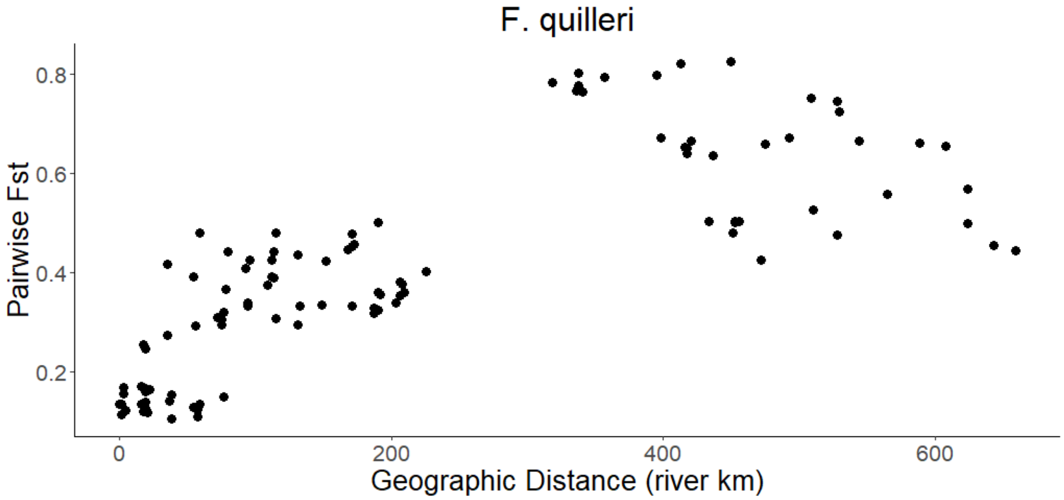

Figure C.1 Empirical relationships between genetic distances (F_{ST}) and geographic distances (river km) between pairs of populations throughout the Colorado River Basin.

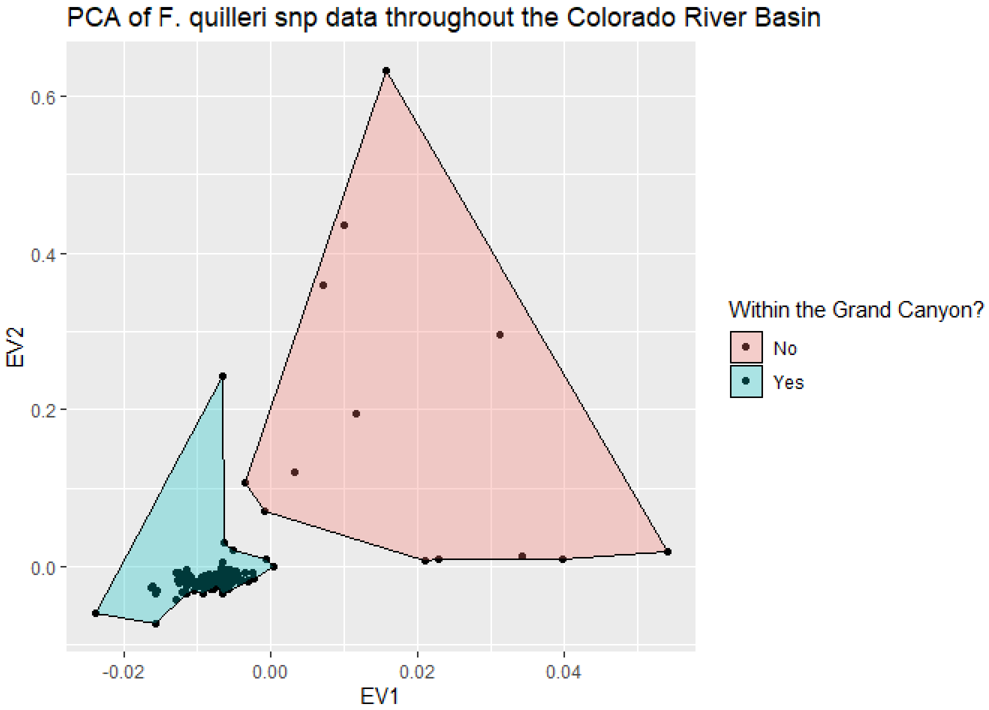

Figure C.2 Principal components analysis of all *F. quilleri* SNP data, showing separation between individuals within the Grand Canyon and those collected in the Upper Colorado River Basin.

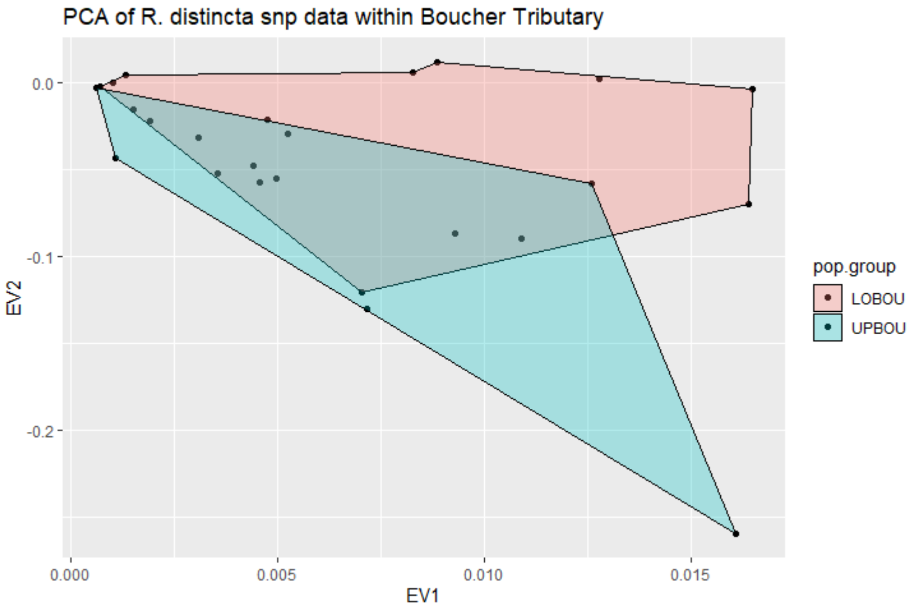

Figure C.3 Principal components analysis of *R. distincta* SNP data from two locations approximately 1.5 km apart within one tributary, Boucher, in the Grand Canyon.

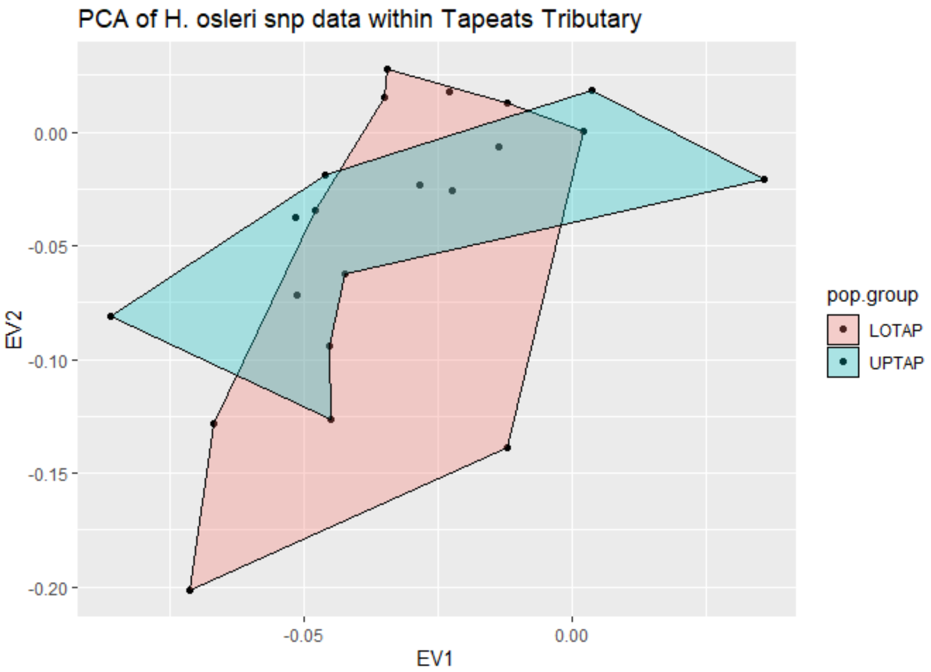

Figure C.4 Principal components analysis of *H. oslari* SNP data from two locations approximately 1.5 km apart within one tributary, Tapeats Creek, in the Grand Canyon.

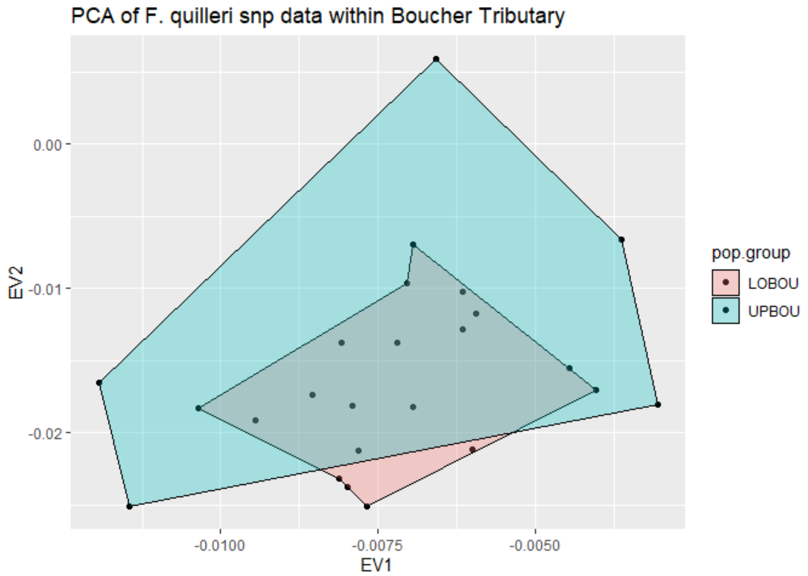

Figure C.5 Principal components analysis of *F. quilleri* SNP data from two locations approximately 1.5 km apart within one tributary, Boucher, in the Grand Canyon.